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Systematic Zoology

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Character Displacement

W. L. BROWN, JR. and E. O. WILSON

IT IS the purpose of the present paper to discuss a seldom-recognized and poorly known speciation phenomenon that we consider to be of potential major significance in animal systematics. This condition, which we have come to call "character displacement," may be roughly described as follows. Two closely related species have overlapping ranges. In the parts of the ranges where one species occurs alone, the populations of that species are similar to the other species and may even be very difficult to distinguish from it. In the area of overlap, where the two species occur together, the populations are more divergent and easily distinguished, i.e., they "displace" one another in one or more characters. The characters involved can be morphological, ecological, behavioral, or physiological; they are assumed to be genetically based.

The same pattern may be stated equally well in the opposite way, as follows. Two closely related species are distinct where they occur together, but where one member of the pair occurs alone it converges toward the second, even to the extent of being nearly identical with it in some characters. Experience has shown that it is from this latter point of view that character displacement is most easily detected in routine taxonomic analysis.

By stating the situation in two ways, we have called attention to the dual nature of the pattern: species populations show displacement where they occur together, and convergence where they do not. Character displacement just might in some cases represent no more than a peculiar and in a limited sense a fortuitous pattern of variation. But in our opinion it is generally much more than this; we believe that it is a common aspect of geographical speciation, arising most often as a product of the genetic and ecological interaction of two (or more) newly evolved, cognate species during their period of first contact. This thesis will be discussed in more detail in a later section.

Character displacement is not a new concept. A number of authors have described it more or less in detail, and a few have commented on its evolutionary significance. We should like in the present paper to bring some of this material together, to illustrate the various aspects the pattern may assume in nature, and to discuss the possible consequences in taxonomic theory and practice which may follow from a wider appreciation of the phenomenon.

Two Illustrations

An example of character displacement outstanding for its simplicity and clarity has been reviewed most recently by Vaurie (1950, 1951). This involves the closely related rock nuthatches *Sitta neumayer* Michahelles and *S. tephronota* Sharpe. *S. neumayer* ranges from the Balkans eastward through the western half of Iran, while *S. tephronota* extends from the Tien Shan in Turkestan westward to Armenia. Thus, the two species come to overlap very broadly in several sectors of Iran (Fig. 1). Outside the zone of overlap, the two species are extremely similar, and at best can be told apart only after careful examination by a taxonomist with some experience in the complex (Vaurie, personal communication). Both species show some geographical variation, and it seems clear from Vaurie's account (1950, Table 5, pp. 25–26) that such races as bear names have been raised for character discordances in various combinations. It therefore appears safe to ignore the subspecies analysis as such and to concentrate on the variation of the independent characters themselves.

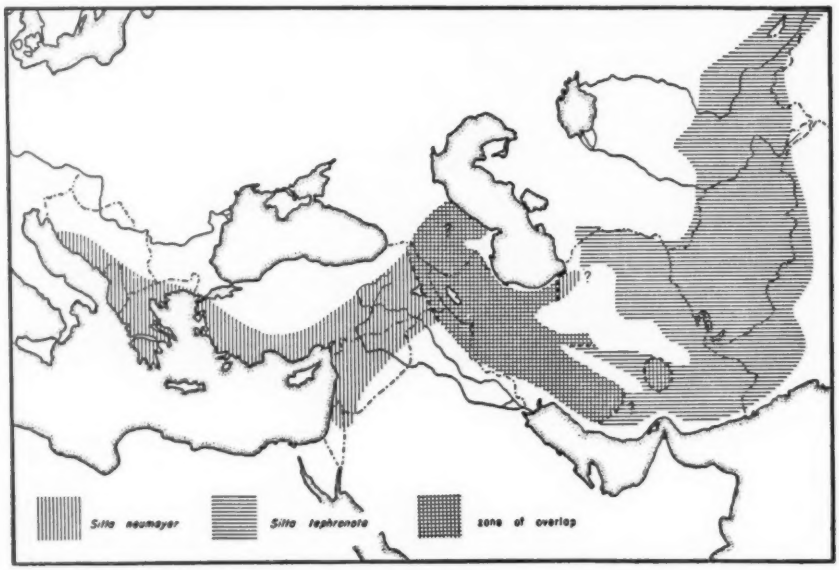

FIG. 1. Distribution of *Sitta neumayer* and *S. tephronota*. (After Vaurie.)

These show quite remarkable displacement phenomena in the Iranian region of overlap between the species, where the two species apparently usually occur in more or less equal numbers (see Fig. 2). In this region, *S. neumayer* shows distinct reductions in overall size and bill length, as well as in width, size, and distinctness of the facial stripe. *S. tephronota*, on the other hand, shows striking positive augmentation of all the same characters in the overlap zone, so that it is distinguishable from sympatric *neumayer* at a glance. Vaurie concludes, we think quite correctly, that the differences within the zone of overlap constitute one basis upon which the two species can avoid competition where they are sympatric. The case of these two nuthatches has already received considerable attention both in the literature and elsewhere, and it bids fair to become the classic illustration of character displacement.

A more complicated case involving multiple character displacement is seen in the ant genus *Lasius* (Wilson, 1955). Where they occur together, in forested eastern North America, the related species *L. flavus* (Fabr.) and *L. nearcticus* Wheeler show differences in the following seven characters: antennal length, ommatidium number, head shape, degree of worker polymorphism, relative lengths of palpal segments, cephalic pubescence, and queen size. In western North America and the Palaearctic Region, where *nearcticus* is absent, *flavus* is convergent to it in all seven characters. In this shift, each character behaves in an independent fashion; e.g., scape length becomes exactly intermediate between that of the two eastern populations, ommatidium number increases in variability and overlaps the range of the two, and queen size changes to that of *nearcticus*. In North Dakota, at the western fringe of the *nearcticus* distribution, the *flavus* population is at an intermediate level of convergence (Fig. 3).

There is some evidence that this dual displacement-convergence pattern is associated with competition and ecological

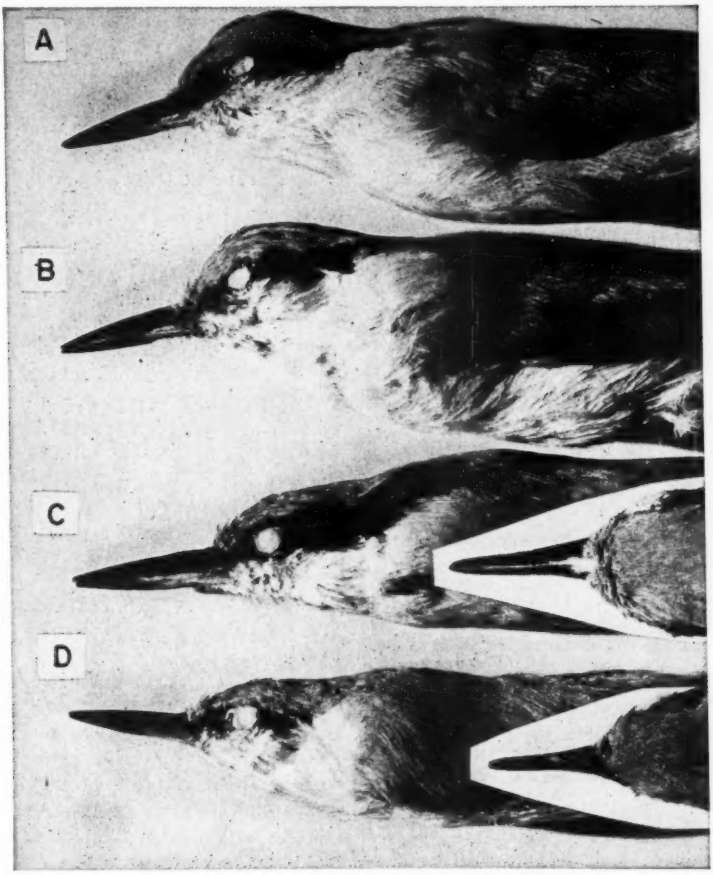

FIG. 2. Size and shape of the bill and facial stripe in *Sitta neumayer* and *S. tephronota*: *A, S. neumayer* from Dalmatia; *B, S. tephronota* from Ferghana; *C, S. tephronota* and *D, S. neumayer,* both from Durud, Luristan, in western Iran. (After Vaurie.)

displacement between the two species. So far as is known, they have similar food requirements. But in eastern North America, where they occur together, *flavus* is mainly limited to open, dry forest with moderate to thin leaf-litter, while *nearcticus* is found primarily in moist, dense forest with thick leaf-litter. There is little information available on the western North American and Asian *flavus* populations, but in northern Europe this species is known to be highly adaptable, preferring open situations, but also occurring commonly in moist forests.

Some Additional Examples

In the following paragraphs we wish to present a number of cases selected from the literature (with two additional unpublished examples) which we have interpreted as showing character displacement. In so doing we are trying to document the thesis that character displacement occurs widely in many groups of animals and in a range of particular patterns. But at the same time we are obliged to give warning, perhaps unnecessarily for the critical reader, that most of these cases in-

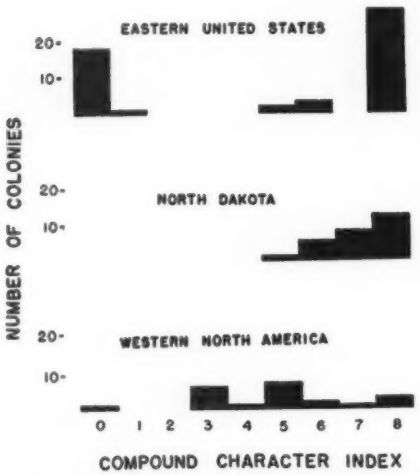

FIG. 3. Frequency histograms of the compound character index of the ants *Lasius nearcticus* (0–1) and *L. flavus* (3–8) in three broad geographic samples. For each colony typical *nearcticus* characters are given a score of 0, typical eastern *flavus* characters a score of 2, and intermediate characters a score of 1. The four characters most clearcut in the eastern United States are used: maxillary palp proportions, antennal scape index, compound eye ommatidium number and head shape. Thus, completely typical *nearcticus* colonies score a total of 0 and completely typical eastern *flavus* 8, with the various ranks of intermediates falling in between (after Wilson, 1955).

volve discontinuously distributed populations, that as a result the species status of these populations with respect to one another has not been ascertained with complete certainty, and that explanations alternative to character displacement are therefore assuredly possible. We ask only that the reader bear through and consider our interpretation in each case.

Birds of the Genus Geospiza. A striking case of character displacement has been described by David Lack in his classic, *Darwin's Finches* (1947). Lack has shown that in the Galapagos certain species of *Geospiza* are often absent on smaller islands, in which case their food niche is filled by other species of the genus. The populations of the latter tend to converge in body size and beak form to the absent species, so much so as to make placement of these populations to species difficult. Lack has demonstrated that body size and beak form are generally important in *Geospiza* in both food getting and species recognition. The dual displacement-convergence pattern we are interested in occurs, at least once, in the following situation. The larger ground-finch *Geospiza fortis* Gould and the smaller *G. fuliginosa* Gould differ from each other principally in size and beak proportion. On most of the islands, where they occur together, the two species can be separated easily by a simple measurement of beak depth, i.e., a random sample of ground-finches (excluding from consideration the largest ground-finch *G. magnirostris* Gould) gives two completely separate distribution curves in this single character. But on the small islands of Daphne and Crossman a sample of ground-finches gives a single unimodal curve exactly intermediate between those of *fortis* and *fuliginosa* from the larger islands. Analysis of beak-wing proportions has shown that the Daphne population is *fortis* and the Crossman population is *fuliginosa;* according to Lack's interpretation each has converged toward the other species, filling the ecological vacuum its absence has created.

Birds of the Genus Myzantha. Among the Australian honey-eaters of the genus *Myzantha,* a light-colored species, *M. flavigula,* occupies the greater part of the arid inland. Toward the wet southwestern corner of the continent, *flavigula* blends gradually into a darker population, usually referred to as "subspecies *obscura.*" In southeastern Australia, in higher-rainfall country, *flavigula* is replaced by two forms—*M. melanocephala,* mostly in the wettest districts, and *M. melanotis* of the subarid Victorian-South Australian mallee district. The southwestern (*obscura*) and one of the southeastern populations (*melanotis*) are ex-

tremely similar, differing by what are described as trifling characters of plumage shading, so that some authors consider them conspecific.

The members of an ornithological camp-out in the Victorian mallee, however, have found that *melanotis* there nests sympatrically with both *melanocephala* and *flavigula,* and that at this place the three behave as distinct species without intergradation. Thus we find the two morphologically very similar forms, *obscura* and *melanotis,* flanking the much more widely distributed and differently colored species, *flavigula,* but showing exactly opposite interbreeding reactions with *flavigula. Obscura* appears to represent merely the terminus of a cline for melanism produced by *flavigula* in the southwest, where, it may be noted, there is no other competing dark form of the same species group (Fig. 4).

Judging by the findings of the mallee observers, *melanotis* is clearly to be regarded as a species distinct from *flavigula,* including the southwestern *obscura* population. In this we follow Condon (1951), and not Serventy (1953), though the latter has furnished the most comprehensive analysis of the situation.

Serventy's dilemma is keyed by his statement that ". . . it would be unreal to treat *melanotis,* obviously so akin to south-western *obscura,* as a separate species from it. . . ." Here one plainly sees the conflict between two species criteria: one based on morphological similarity, and one on interbreeding reaction in the zone of sympatry.

From the data presented, we interpret the *Myzantha* situation as a case of character displacement. *M. flavigula* tends to produce, in the less arid extremities of its range, populations with darker plumage. In the southwest, it has done just this; presumably, melanism is connected adaptively in some way, directly or indirectly, with increased moisture ("Gloger's Rule"), or plant cover, or both. In the southeastern mallee, however, the melanistic tendencies presumed to be latent or potential in *flavigula* toward the wetter extremes of its range are suppressed in the presence of the darker species *melanotis* (and possibly also *melanocephala*). It would be interesting to know more about

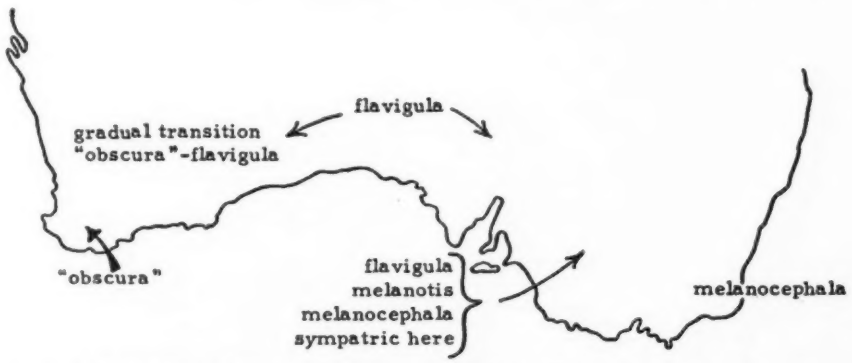

FIG. 4. Map showing the geographical relationships of three species of the bird genus *Myzantha* in southern Australia, based on the discussion of Serventy, 1953. *M. flavigula,* the light-colored bird of arid central Australia, grades into a darker population ("race *obscura*") in southwestern higher-rainfall districts. In southeastern Australia, in the Victorian mallee belt, transitional and mixed ecological conditions allow three non-intergrading species to breed side by side: *M. flavigula; M. melanotis,* a species characteristic of the mallee scrub; and *M. melanocephala,* a southeastern bird of the higher-rainfall districts. *M. melanotis* and the *"obscura"* population are extremely similar, and have been considered synonymous or at least conspecific in the past.

the ecological distribution, food, and habits of the three *Myzantha* species within the region where they occur together.

Parrots of the Genus Platycercus. Serventy (1953) also reviews, among other cases that may involve character displacement, the situation in the rosellas of southeastern Australia (Fig. 5). The crimson rosella (*Platycercus elegans*) is a species of the wooded eastern areas—mostly those with higher rainfall nearest the coast. On Kangaroo Island, off the coast of South Australia, occurs a crimson population that appears to be *elegans* from a strictly morphological viewpoint. Beginning on the mainland opposite Kangaroo Island is a cline connecting the crimson form to an inland, arid-country yellow form (*P. flaveolus*) inhabiting the red gums of the rivers and dry creeks in the Murray-Darling Basins. However, in the Albury district of the upper Murray River and elsewhere up the other rivers, *flaveolus* overlaps or closely approaches the true southeastern *elegans* along a wide front without interbreeding (for a recent detailed account, see Cain, 1955).

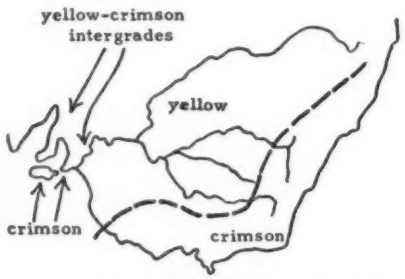

FIG. 5. Map showing the approximate distribution of color forms of the rosellas (parrots) of the *Platycercus elegans* complex in southeastern Australia. The heavy pecked line indicates roughly the inland margin of the southeastern highlands and the higher-rainfall districts, and also the inland limit of the range of the crimson-trimmed *P. elegans*. Inside this line, along the upper reaches of the Murray-Darling river systems, the closely related *P. flaveolus*, a yellow-trimmed form, approaches and may even meet the range of *P. elegans* at some points without producing intergrades. Downstream, *P. flaveolus* grades through a series of intermediately-colored populations culminating in the crimson-trimmed flocks of Kangaroo Island, which are apparently outwardly indistinguishable from those of the true eastern *elegans*. (Adapted from Cain, 1955.)

It is interesting to note that the cline from yellow to crimson in South Australia follows broadly the regional increase in moisture and luxuriance of forest vegetation; both rise to peaks in the ravines at the western end of Kangaroo Island. We suggest that the South Australian clinal population on the mainland, and probably even the crimson populations of Kangaroo Island, are referable to *flaveolus*, which can here produce a wet-adapted crimson form free of displacement pressure from *elegans*.

Birds of the Cape Verde Islands. Bourne (1955) in his review of the birds of the Cape Verde Islands, has presented several cases of character displacement so concisely and pointedly that we can quote him directly:

> The two shearwaters [breeding in the Cape Verde Islands], Cory's shearwater *Procellaria diomedea* and the Little Shearwater *Procellaria baroli*, take similar foods (fish and cephalopods) differing only in size; competition for food between the two species is reduced by the development of different breeding seasons. Elsewhere in its range *Procellaria diomedea* breeds at the same stations as the medium Manx Shearwater *Procellaria puffinus*, which takes similar foods but breeds slightly earlier. There is a dramatic difference in size, and particularly the size of bill, between those races of *Procellaria diomedea* which breed with *Procellaria puffinus* and the form *[P. diomedea] edwardsi* which breeds alone at the Cape Verde Islands, the latter having a bill exactly intermediate in size between that of the northern races and that of *Procellaria puffinus*. It seems likely that *edwardsi* takes the food that is divided between both species elsewhere. It may be remarked that one race of *Procellaria puffinus*, *mauretanicus* of the Balearic Islands, avoids competition with *Procellaria diomedea* by breeding unusually early and leaving the area when the larger species prepares to nest; it is significant that this is the only race of the

species which has a large bill resembling that of *P. d. edwardsi*. It would appear that the bill-size and the breeding seasons of these shearwaters vary with the amount of competition occurring between different species breeding at the same site. . . .

Where the two kites *Milvus milvus* and *Milvus migrans* occur together the latter is the species which commonly feeds over water. The race of *Milvus milvus* found in the Cape Verde Islands closely resembles *Milvus migrans* in the field, and very commonly feeds along the shore and over the sea. It may replace *Milvus migrans*, but it seems likely that with the Raven *Corvus corax*, which also abounds along the shore, it replaces the gulls *Larus* spp. which usually scavenge along the shore elsewhere but have failed to colonize the barren coast of the islands.

Bourne's opinion concerning which species are replaced is a little confusing in this case, since elsewhere *Milvus*, notably *M. migrans* in India, often tends to replace or at least dominate the gulls in scavenger-feeding situations around seaports (Brown, personal observation). The absence of *migrans* seems to us the probable chief reason for the convergence characteristics in the Cape Verde Islands populations of *milvus*.

Bourne cites one additional case:

> The Cane Warbler *Acrocephalus brevipennis* [a species precinctive to the Cape Verde Islands] is closely related to large and small sibling species *Acrocephalus rufescens* and *A. gracilirostris* which occur together in the same habitats on the [African] mainland. Where the ranges of these two species overlap they are sharply distinct in size and voice; where they occur apart these distinctions are less marked (Chapin, 1949). *A. brevipennis* is probably related to the larger species, *A. rufescens*, but in the absence of the smaller species it is exactly intermediate in all its characters except the bill, which is large, resembling that of *A. rufescens*. The large bill may be part of the general trend seen on islands, or a consequence of competition for food with the smaller *Sylvia* warblers.

Birds of the Genus Monarcha. Mayr (1955 and personal communication) has described a case of displacement in the monarch flycatchers of the Bismarck Archipelago. *Monarcha alecto* and *M. hebetior eichhorni* occur together through the main chain of the Bismarcks, from New Britain north onto New Hanover, but beyond, on isolated St. Matthias, *M. hebetior hebetior* occurs alone; this last is an ambiguous variant combining several features of *alecto* and *eichhorni*. Mayr suggests the following evolutionary scheme: *hebetior* differentiated from *alecto* as an isolate on St. Matthias and later reinvaded the range of *alecto* on New Britain and New Ireland, where it diverged further under displacement pressure from the latter until it became the present *eichhorni*.

It seems to us that this situation can be more simply explained by assuming that the Bismarcks were first populated by a stock which evolved within the Archipelago and became the species *hebetior*. The later entry of *alecto* into the chain was followed by the displacement of *hebetior* as far as the sympatry extended, leaving the St. Matthias isolate to represent the undisplaced relict of the original *hebetior*.

Fishes of the Genus Micropterus. The two basses *Micropterus punctulatus* and *M. dolomieu* have ranges which include a large part of the eastern United States and are mostly coextensive (Hubbs and Bailey, 1940). Of the two, however, only *punctulatus* is known to occur in Kansas, western Oklahoma, and the Gulf States south of the Tennessee River drainage system. In the Wichita Mountains of western Oklahoma there is a population, described as *M. punctulatus wichitae*, which is intermediate between typical *punctulatus* and *dolomieu*. Its affinity to *punctulatus* is shown by the fact that in a number of characters it grades without a break into *punctulatus*, so that some specimens are indistinguishable from typical *punctulatus*, and in its agreement with *punctulatus* in the critical character of scale-row counts. Hubbs and Bailey seem to favor the theory of a hybrid origin for *wichitae*, but they consider this "no more plausible than the view that

the similarities between *wichitae* and *dolomieu* are caused by parallel development, or the view that *wichitae* is a relict of a generally extinct transitional stage between *punctulatus* and *dolomieu.*" We, of course, are inclined to favor parallel development, resulting specifically from the absence of the displacing influence of *dolomieu,* as the simplest and most plausible explanation.

Away to the south, many of the Texas populations of *punctulatus* are peculiar in showing converging trends toward *dolomieu,* but less strongly, so that Hubbs and Bailey consider them as possible intermediates between *punctulatus* and *wichitae.* In northern Alabama and Georgia there is a form described as a distinct species (*M. coosae*), which combines some of the characters of *punctulatus* and *dolomieu,* besides showing some peculiar to itself. *Coosae* is completely allopatric to *dolomieu,* and there is some evidence that it may hybridize extensively with the sympatric *punctulatus.* We should like to suggest the possibility here that *coosae* is conspecific with *punctulatus* and represents a section of the *punctulatus* population tending to converge toward *dolomieu* where that species is absent.

In summary, it appears to us likely that *wichitae,* the Texas populations, and possibly even *coosae,* each of which shows intermediate characters, are not products of introgressive hybridization, but may instead represent true *punctulatus* stocks that have tended to converge toward *dolomieu* in the absence of displacing influence from that species.

Frogs of the Genus Microhyla. W. F. Blair (1955) concludes from his study of two North American frogs of the genus *Microhyla:*

> The evidence now available shows that there are geographic gradients in body size in both *Microhyla olivacea* and *M. carolinensis.* The former species shows a west to east decrease in body length, while the latter shows an east to west increase. The clines are such, therefore, that the largest *carolinensis* and the smallest *olivacea,* on the average, occur in the overlap zone of the two species. This pattern of geographic variation in body size parallels the pattern of geographic variation in mating call reported by W. F. Blair (1955) [in press] in which the greatest call differences in frequency and in length occur in the overlap zone. One of these call characteristics, frequency, probably is directly related to body size, for smaller anurans of any given group tend to have a higher pitched call than larger ones of the same group. The other, length of call, appears unrelated to size.
>
> The differences in body size, like those in mating call, belong to a complex of isolation mechanisms (W. F. Blair, 1955) which tends to restrict interspecific mating in the overlap zone of the two species. The existence of the greatest size differences as well as the greatest call differences where the two species are exposed to possible hybridization supports the argument (*op. cit.*) that these potential isolation mechanisms are being reinforced through natural selection.

Frogs of the Genus Crinia. A most interesting case in the Australian genus *Crinia* has recently been called to our attention by A. R. Main (*in litt.*). Where they occur together in Western Australia, as around Perth, the two species *C. glauerti* and *C. insignifera* have markedly different calls. *C. glauerti* has a rattling call resembling "a pea falling into a can and bouncing"; oscilloscope analysis shows this to consist of evenly spaced single impulses at the rate of about 16 per second. *C. insignifera* produces a call "similar to a wet finger being drawn over an inflated rubber balloon . . . we refer to this call as a 'squelch.'" Oscilloscope analysis shows the squelch to have a duration of about 0.25 second and to consist of impulses crowded together. Around Perth and in other localities where it is sympatric with *insignifera, glauerti* individuals are occasionally heard to produce the beginnings of the "squelch" by running 12–15 impulses together, but this occurrence is extremely rare. Along the south coast of Western Australia, however, where *glauerti* occurs alone, the call is commonly modified by running 30 or more single impulses together to produce a squelch almost identical to the ear with that of *insignifera.* Thus, in effect, where this species occurs alone it has extended

the variability of its call to include the sounds typical of both species. According to Main, the two species show color differences in the breeding males and different ecological preferences; laboratory crosses show reduced F_1 viability. It seems evident to us (Brown and Wilson) that displacement in this case is associated with the reinforcement of reproductive barriers, the breakdown of which would result in inferior hybrids. This aspect will be discussed more fully in a later section.

Ants of the Genus Rhytidoponera. The ants of the Australian *Rhytidoponera metallica* group (revised by Brown, ms.) are widespread and often among the dominant insects of given localities. The common greenhead (*R. metallica*) is the most successful species—a metallescent green or purple ant adapted to a variety of habitats ranging from desert to warm, open woodland, and the only species of the group at all abundant across the dry interior of Australia. In the southeastern and southwestern ("Bassian") corners of the continent, where the rainfall is higher and luxuriant forests occur, *metallica* is replaced by similar species of the same group that nearly or quite completely lack metallic coloration (Fig. 6).

In the east, two such species make the replacement, *R. tasmaniensis* Emery and *R. victoriae* André. *R. tasmaniensis* is the larger of the two, has the fine gastric sculpture of *metallica*, and is usually reddish brown, with bronzy-brown gaster. It is virtually identical with *metallica*, except for color. *R. victoriae* is smaller, more blackish, and has relatively coarser gastric striation. *R. tasmaniensis* is found in a variety of woodland situations, but apparently is excluded from the very wettest forests, which are occupied by *victoriae*. Nevertheless, the two species exist in abundance side by side over large parts of southeastern Australia without a sign of interbreeding. At some points, such as on the moist temperate grasslands west of Melbourne, both species occur together with *metallica*, but maintain their distinctness.

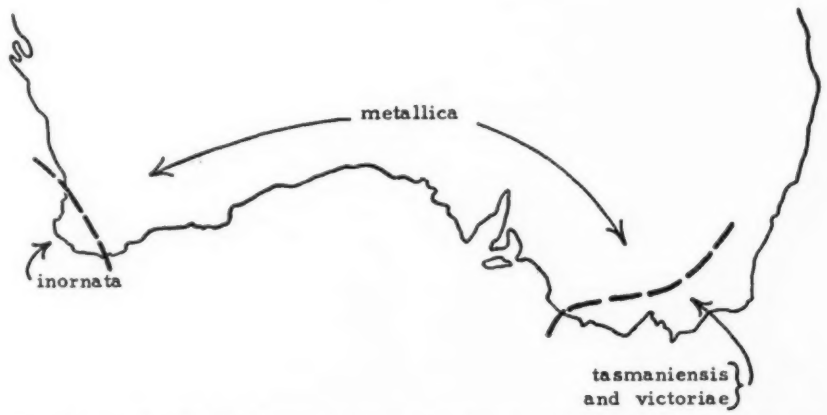

FIG. 6. Map showing the approximate distribution in southern Australia of four closely related common species of ants of the *Rhytidoponera metallica* group. *R. metallica* is nearly or quite the only representative of its group in the more arid central regions, and occurs in open situations in the southeast and southwest as well. In the moister forests of the southeast, *metallica* is replaced by the small, dark *R. victoriae* and the larger, more reddish *R. tasmaniensis*, which frequently occur side by side in the same localities. In the mesic wooded areas of the extreme southwestern corner of Australia, *metallica* is replaced by *R. inornata*, a distinct species which in size and color resembles closely, and broadly overlaps in variation, the two eastern forest species.

In the southwestern corner of Australia, *metallica* is replaced in the wetter parts of the region by non-metallescent *R. inornata* Crawley (though the two species overlap in the Darling Range and undoubtedly elsewhere). The interesting feature here is that *R. inornata* varies in size and color so as to cover the variation in these attributes of both southeastern non-metallic species, *tasmaniensis* and *victoriae*. In fact, one might speak of the two southeastern forms as mutually-displacing equivalents of the southwestern *inornata*, the latter being nearest the generalized type of the group because it has never suffered close competitive pressure and the character displacement that helps to relieve that pressure. This example illustrates the existence of a dual character-displacement pattern where the convergent population is clearly at, or above, the species level.

Slave-making Formica *Ants.* A simpler case in the ants involves the famous Holarctic slavemakers of the *Formica sanguinea* group. In a recent revision (Wilson and Brown, 1955) only three really distinct species are recognized in the group: *F. sanguinea* Latreille, widely distributed through temperate and northern Eurasia, where it is the only species; *F. subnuda* Emery, of boreal and subboreal North America; and *F. subintegra* Emery, ranging through temperate North America and overlapping the range of *subnuda* in the northern United States and along the Rocky Mountain chain.

The two most different forms are *subnuda* and *subintegra*, which can be separated on several external characters. *F. sanguinea* is closely related to *subnuda* in form and habits and is treated as a separate species only arbitrarily, on the basis of slight morphological discontinuities. At the same time, *sanguinea* has pilosity intermediate between that of the two American species, and its clypeal notch, a second important diagnostic character, is more like that of *subintegra* than like that of *subnuda*. We have interpreted this pattern to represent a displacement of *subnuda* away from *subintegra* where these two species meet and interact, while the Palaearctic equivalent of *subnuda* (i.e., *sanguinea*) has tended to converge toward *subintegra* as a consequence of its filling the "adaptive vacuum" which a companion species might otherwise occupy. Of course in this case, as in all others under present consideration, there is no way of determining how much "displacement" has occurred as a process in the sympatric populations as opposed to "convergence" in the unispecific one. The final pattern observed may in fact be the result of one of these two processes alone.

American Scarabaeid Beetles. Howden (1955, p. 207) discusses the status of two geotrupine beetles considered by him to represent subspecies of the species *Eucanthus lazarus* (Fabricius). His *E. l. lazarus* is stated to range widely over the United States, but records from the Gulf States, excepting Florida, are scanty. *E. l. subtropicus* Howden, on the other hand, is restricted to the southeastern states, and is best represented in Florida, Georgia, Alabama and neighboring states.

Howden is puzzled by the apparent fact that "intermediates" between the two forms came from areas "not bordering the Gulf of Mexico," despite the circumstance that it is in this region that the main overlap falls. Intergrades came from areas "on the East Coast," and from Miami, Florida, and, "Occasional northern specimens appear to exhibit most of the characters of *subtropicus*." However, in particular limited localities, presumably near or in the zone of overlap, Howden was able to name the populations one way or the other with little difficulty.

Although the situation in the Florida Peninsula is not clear from Howden's account, the "intermediate" and more typical-appearing *E. l. lazarus* occurring together with *subtropicus* in the Miami area may really represent undisplaced populations of *subtropicus*. If this is the case, then we would favor Howden's alterna-

tive interpretation, and consider *lazarus* and *subtropicus* as closely related but distinct species.

Crabs of the Genus Uca. Jocelyn Crane (in Allee *et al.*, 1950, p. 620) notes that in fiddler crabs of the genus *Uca* differentiation in behavior and often in the coloration of the male is greater if the species are found together than if they are found in different habitats or regions.

The Evolution of Character Displacement

Divergence between two species where they occur together, coupled with convergence where they do not, is a pattern that strongly suggests some form of interaction in the evolutionary history of the pair. The usual case may be one in which the members of the pair are cognate (derived from the same immediate parental population) and have recently made secondary contact following the geographical isolation that has mediated their divergence to species level. In such cases, the "terminal" populations, to which overlap does not yet extend, are not affected by the contact and remain closely similar to each other. But where contact has been made, there are two important ways in which the sympatric populations can interact to augment their initial divergence.

The first type of interaction might best be termed *reinforcement*[1] of the reproductive barriers. It may happen that the species continue to interbreed to some extent, and either the resulting inseminations are ineffectual, or the hybrids produced are inviable or sterile, resulting in what geneticists have termed "gamete wastage." Consequently, any further ethological or genetic divergence reducing this wastage will be strongly favored by natural selection (Dobzhansky, 1951; Koopman, 1950; Kawamura, 1953).

Of conceivably equal or greater importance is the process of *ecological displacement*. It seems clear from an *a priori* basis that any further ecological divergence lessening competition between the overlapping populations will be favored by natural selection if it has a genetic basis (Mayr, 1949). That such a process actually occurs is suggested by abundant indirect evidence from ornithology (Lack, 1944), as well as the cases already cited above.

It seems unnecessary to go into a detailed discussion of these previously elaborated concepts, except to point out that secondary divergence of this nature inevitably entails phenotypic "characters" of the type employed in ordinary taxonomic work. Character displacement therefore may be considered as merely the aspects of such divergence that are recognizable to the taxonomist and some other favored organisms. It is interesting to note that the tendency toward displacement of characters is opposed by the pressure for mimicry. One can imagine some elaborate interactions between the two tendencies, particularly in the evolutionarily fertile tropics.

Competition

The concept of competition has been the focus of much important disagreement among ecologists and other biologists, and it deserves close and persistent investigation. However, were it not that Andrewartha and Birch (1954) criticize the use of the concept by Lack and others to explain distribution and variation of birds and other animals, we might well have avoided discussing it here altogether. Andrewartha and Birch (p. 25) seem to consider that competition is an idea of lesser, perhaps even negligible, importance in biology. They think that the tendency for closely related species to inhabit different areas or exploit different ecological niches (as reported, for instance, by Lack) may conceivably have originated from causes "quite different" from competition. They do not offer alternatives that seem to us anything like as satisfactory as Lack's hypotheses.

Andrewartha and Birch make a point

[1] *Reinforcement* is a familiar term in psychology that has been applied to speciation processes (Blair, 1955).

when they ask for more direct evidence for the action of competition, but it is clear that they have failed to appreciate the amount of evidence that does exist in the literature. However, interspecific competition of the direct, conspicuous, unequivocal kind is apparently a relatively evanescent stage in the relationship of animal individuals or species, and therefore it is difficult to catch and record (just as is the often parallel crisis in the rise of reproductive barriers between two newly diverging species). What we usually see is the result of an actually or potentially competitive contact, in which one competitor has been suppressed or is being forced by some form of aggressive behavior to take second choice, or in which an equilibrium has been established when the potential competitors are specialized to split up the exploitable requisites in their environment. A third possible result is the dispersion of potential competitors in space (Lack, 1954). Surely the cases of character displacement we have considered above, especially those for which we have some ecological data, are pertinent examples of correlation between sympatry (with the possibility of competition) and genetic fixation of specializations resulting in the avoidance of competition. The respective convergent unispecific populations outside the sympatric zones are the "controls" for these observations.

The case in which Lack (1944) cites the distribution of the chaffinches (*Fringilla*) in the Canary Islands is held up to special criticism by Andrewartha and Birch. Lack demonstrates that *F. teydea,* endemic to the islands of Gran Canaria and Tenerife, occupies only the coniferous forests at middle altitudes. On the same islands there also occurs a form of the widespread *F. coelebs,* presumably a relatively recent arrival from the Palaearctic mainland, but this bird occurs only in the tree-heath zone above, and in the broadleaf forests below, the coniferous belt. On the island of Palma, however, *F. teydea* is absent, and there a form of *F. coelebs* occupies the coniferous forest as well as the broadleaf zone. Andrewartha and Birch conclude that, "So far as the case is stated, there is no direct evidence that the two species could not live together if they were put together." It is obvious from this that Lack's critics are not going to be satisfied by any ordinary kind of evidence.

What emerges starkly from contemporary discussion of "competition" is the great variation in the meanings with which different authors freight the word. Andrewartha and Birch, while differing with Nicholson (1954) on most important points, do manage to agree with him that the correct kernel of meaning of competition is contained in the expression "together seek." We would adopt the part of their definition that deals with the common striving for some life requisite, such as food, space or shelter, by two or more individuals, populations or species, etc. This seems to us to be close to the definitions preferred by the larger dictionaries we have consulted.

But Andrewartha and Birch, following many other writers, allow their competition concept to include another idea—that expressing direct interference of one animal or species with the life processes of another, as by fighting. On the surface, this inclusion of aggression as an element of competition may seem to some familiar and reasonable, but we wonder whether the concept of competition could not be more useful in biology if it were more strictly limited to "seeking, or endeavoring to gain, what another is endeavoring to gain at the same time," the first meaning given in *Webster's New International Dictionary, Second Edition, Unabridged.* It is noteworthy that competition as defined by this dictionary fails to include the idea of aggression in any direct and unequivocal way.

It may therefore be more logical in the long run to regard the various kinds of aggression between potential competitors (the outcome of which is so often predictable) as another method, parallel with

character displacement and dispersion—and genetically conditioned in a similar fashion—by which organisms seek to lessen or avoid competition. Surely it is significant that aggressive behavior often seems most highly developed in cases where a conspecific, or closely related, potential competitor occurs with the aggressor, yet shows little or no displacement in behavior or form. In contrast are the many cases of complete mutual tolerance shown by closely related organisms that live side by side and are differentially specialized in behavior or form.

Character Displacement versus *Hybridization*

Since both divergent and "intermediate" populations are involved in the displacement patterns we have been describing, it is clear that the convergent populations might easily be mistaken as representing products of interspecific hybridization between the two species displacing each other. This is especially true if the convergent populations are small and isolated, or if only a single one is developed. Lack, for instance, in an early paper (1940) interpreted the Daphne and Crossman populations of *Geospiza* as being of hybrid origin, changing his mind only after he had begun to consider more fully the influence of competition on speciation (in *Darwin's Finches,* 1947).

To take another possible example, Miller (1955) describes what he calls a "hybrid" between the woodpeckers *Dendrocopos scalaris* and *D. villosus.* This specimen, a female, was shot in the Sierra del Carmen, Coahuila, Mexico, at about 7000 feet altitude, near the lower limits of the coniferous belt capping the Sierra. Up to, or near, this altitude, Miller found the Sierra to support a population of *scalaris,* but despite intensive collecting, he found no sign of occupancy by the other putative parent species, *villosus. D. scalaris* reaches a higher point in these mountains than it usually does in the neighboring regions of desert scrub and bottomland—its habitat wherever it has been studied—in Mexico, Arizona, New Mexico and parts of Texas. In general, the *villosus* populations of this part of North America are restricted to the higher coniferous belts, but *villosus* and *scalaris* are in contact at some stations where pinyon-oak-juniper meets coniferous forest. Presumably *scalaris* extends farther vertically in the Sierra del Carmen because *villosus* is not present to limit its upward expansion. According to Miller, *villosus* probably does not occur within 200 miles of the Sierra at the present time.

The specimen, thoroughly described and figured by Miller, is indeed intermediate in many respects between the *scalaris* and *villosus* of northern Mexico. However, there seems to be nothing in the information presented to prevent one's interpreting this as a large, unusually dark specimen of *scalaris,* instead of as a hybrid. There is no good reason to deny the possibility that *scalaris* can produce somewhat *villosus*-like variants at the upper limits of its range when *villosus* is absent.

Other examples we have already cited in the present paper show the difficulty in deciding between displacement and hybridization where the species involved are incompletely known. This situation adds considerable complication to the analysis of interspecific hybridization in nature, for it is clear that the alternative explanation of displacement should at least be taken into account.

One thing seems certain; the "hybrid index," better called "compound character index," can by itself be no sound indication that the situation plotted really involves hybridization. This leads us to ask whether even such elaborate and beautifully documented studies of "hybrid" situations as that made by Sibley (1950, 1954) on the towhees of southern Mexico (*Pipilo erythrophthalmus s. lat.* and *P. ocai*) are not really just illustrations of character displacement. In some of the higher mountains of the southeast (Orizaba, Oaxaca), the two very differently colored forms (species) meet but

remain distinct. Farther west are found various populations that apparently grade between the extreme *erythrophthalmus* form and the *ocai* form to various degrees of intermediacy, as expressed by Sibley in his "hybrid index."

Some of the *ocai*-form populations at the western end of the range (*P. ocai alticola*) are stated to be distinct from the other races of *ocai* by a characteristic melanization of the head region, which Sibley thinks is due to introgression from *erythrophthalmus* populations found to the north in the Sierra Madre Occidental. Despite this indication of introgression, the western populations at the *ocai* end of the gradients studied are indexed at, or extremely close to, zero, the figure indicating a population of "pure" *ocai*. Aside from what seems to be a variation in "purity" standards for *ocai* here, it is interesting to note that the western populations and those others among the apparent intermediates of the southern Plateau Region can all conceivably, on present evidence, be interpreted as *erythrophthalmus* that have converged toward *ocai* in the absence of the "true" *ocai* form represented by the upland, sympatric southeastern samples.

It seems possible that some strong selective pressure may be acting in the southern Plateau region to produce an *ocai* coloration-type in finchlike birds, and that *erythrophthalmus* may yield to this pressure wherever the true *ocai* is absent in this area. A very *ocai*-like bird of a related genus, *Atlapetes brunneinucha*, reaches the northern limit of its range in the southern Plateau area, and it is possible that the striking similarity marks some adaptive relationship to which both it and the *Pipilo* stock respond. It might even be that mimicry is involved between the sympatric *Atlapetes* and *Pipilo* stocks, although this is nothing more than the sheerest speculation in view of our very incomplete knowledge of the relative distribution of the two forms and other aspects of their biology and their environment, including their predators. At any rate, character displacement must for the time being be considered a reasonable alternative explanation of the variation of southern Mexican *Pipilo* in this group.

It may perhaps be argued that the "hybrid" populations of *Pipilo* are more variable than the presumed parental populations, and that this in itself is a strong indication of hybridization. We do not believe, however, that the case should be decided on this kind of evidence. To start with, tailspot length, the one character used in Sibley's study that has also been analyzed at length in other populations of *P. erythrophthalmus*, shows very considerable variation in areas far removed from the likely influence of *ocai*. According to the data of Dickinson (1953), the Florida population ("race *alleni*") has a coefficient of variation in this character of about 22 in the male; the range of variation is from 6.1 to 27.5 mm. The northeastern (nominate) race shows a corresponding coefficient of about 12, with a range of variation of from 24.0 to 55.0 mm. Furthermore, the chestnut-tinted pileum characteristic of *ocai-erythrophthalmus* "hybrids" occasionally crops up in the eastern North American samples of *erythrophthalmus*. But even if it were true that variation in the direction of *ocai* could be demonstrated only in the *ocai* "area of influence," this could not be taken as proof of hybridization, because an increase in variation is also a common quality of the "convergent" populations in character displacement patterns.

Character Displacement and Taxonomic Judgment of Allopatric Populations

Foremost among the problems of taxonomic theory today is the tantalizing conundrum concerning the status of the allopatric (isolated) population. Few authors hesitate to assign such populations either subspecific or specific rank, and most, it is hoped, appreciate the fact that their decisions are essentially arbitrary. As Mayr (1942) says, "The decision as to whether to call such forms species or sub-

species is often entirely arbitrary and subjective. This is only natural, since we cannot accurately measure to what extent reproductive isolation has already evolved." There does not seem to be any definable threshold between polytypic species composed of such subspecific "units" and the superspecies composed of allopatric sister species. However, it is entirely possible that by the time an isolated population attains an ascertainable level of character concordance, it has already passed the species line; i.e., the more sharply defined an isolated subspecific population is by conventional standards, the less likely it is to be infraspecific in reality.

The phenomenon of character displacement should be borne heavily in mind in considering this matter of allopatric populations. If the present conception is correct, related sympatric species will generally show more morphological differences than similarly related allopatric ones. Hence the degree of observed difference between sympatric species cannot be considered a reliable yardstick for measuring the real status of related allopatric populations, nor can the differences among the latter be taken too seriously as indications of their relationships. In fact, the morphological standards set for determining which completely allopatric populations have reached species level may be much too strict in current practice. Despite impressions that might be gained from recent literature, many systematists have realized that in different allopatric populations (of the same species-group or genus), the degree of morphological divergence may be poorly correlated with the amount of reproductive isolation holding between them (Moore, 1954; Kawamura, 1953). In other words, where there is any question whatsoever about the objective species status of two closely related but geographically separated populations, morphology alone cannot be expected to answer it definitely.

Unfortunately, allopatric species or "subspecies" designated as such on a purely morphological basis frequently enter into theoretical discussions as though they were objectively established realities, when in fact they are usually no more than arbitrary units drawn for curatorial convenience.

Summary

Character displacement is the situation in which, when two species of animals overlap geographically, the differences between them are accentuated in the zone of sympatry and weakened or lost entirely in the parts of their ranges outside this zone. The characters involved in this dual divergence-convergence pattern may be morphological, ecological, behavioral, or physiological. Character displacement probably results most commonly from the first post-isolation contact of two newly evolved cognate species. Upon meeting, the two populations interact through genetic reinforcement of species barriers and/or ecological displacement in such a way as to diverge further from one another where they occur together. Examples of the phenomenon, both verified and probable, are cited for diverse animal groups, illustrating the various aspects that may be assumed by the pattern.

Character displacement is easily confused with a different phenomenon: interspecific hybridization. It is likely that many situations thought to involve hybridization are really only character displacement examples, and in cases of suspected hybridization, this alternative should always be considered. Displacement must also be taken into account in judging the status (specific *vs.* infraspecific) of completely allopatric populations. It is clear that, in the case where the species are closely related, sympatric species will tend to be more different from one another than allopatric ones. Thus, degrees of difference among related sympatric populations cannot be used as trustworthy yardsticks to decide the status of apparently close, allopatric populations.

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Transliteration of Greek to Latin in the Formation of Names of Zoological Taxa

R. E. BUCHANAN

MOST of the names of taxa of animals are derived from the Greek, as are also many of the specific (trivial) and subspecific names. Under the Zoological Rules the Greek words are to be transliterated and treated as Latin words. Throughout the history of modern zoology there has been the tacit assumption that the classic precedent as established by the Latins should be followed in such transliteration. Linnaeus himself stated that when Greek names are transliterated into Latin "the equivalents used by the Romans from all time must be adopted in representing the Greek letters." He twice outlined in part the "classic" rules and gave examples of good form. However, an examination of the names of taxa proposed in zoology shows that in practice there exist variations in transliteration that have led to confusion.

Proposed here is the correction and emendation of the current outlined schema appended to the Zoological Rules of Nomenclature for the transliteration of Greek words into Latin form suitable for use in the formation of names of taxa in zoology. Directives and a tabulation for such transliterations have been published in connection with the several editions and reprintings of the Zoological Rules, as in the Smallwood mimeographed "International Rules of Nomenclature" (1915), Proceedings of the Biological Society of Washington (1926), Schenck and McMaster's *Procedure in Taxonomy* (1948 revision), and Follett's *Unofficial Interpretation* (1955). Apparently, this tabulation (after revision?) is to be included in the Second Schedule (formerly Appendix) of the revised Rules. This formulation has evidently been used with succeeding editions without careful scrutiny. When examined it is found in several particulars to be incorrect, misleading, and inadequate. It is assumed to be a guide to classical usage in Greek-Latin transliteration. An analysis of the errors and omissions of the present Schedule is not necessary here. Instead the following emended tabulation is proposed for consideration for inclusion as a replacement in the forthcoming Second Schedule of the Rules. It is believed to be much more inclusive than the previously published tabulation, to have eliminated certain errors, and to represent classical usage. It should be scrutinized by those who have both classical and biological training, and, when suitably emended, considered for approval for the guidance of zoological nomenclators and taxonomists.

Greek Α, α (alpha). Latin *A, a*

ἀκανθίων=*acanthion* ....*Acanthion*

The Greek α is the first letter of two Greek diphthongs:

αι=*ae* λιμναῖος=
limnaeus .....*Limnaea*

Rarely and less correctly it is transliterated:

αι=*ai* αἶρα=*aira* .....*Airaphilus*

Occasionally the Greek sequence αϊ occurs, as in:

Μαΐος=*Maïus,* in which it is not a diphthong..*Maïa*

Occasionally *αι=ae* has been incorrectly transliterated as *e*. *αἷμα=haema* as in *Hematospiza* for *Haematospiza*

αυ=au γλαυκός=
glaucus .....*Glaucus*
ἁ=ha ἅλιος=halius .....*Haliophis*
αἱ=hae αἷμα=haema ....*Haematochiton*

Greek Β, *β* (beta). Latin *B, b*

βάλανος=balanus .....*Balanonema*

Greek Γ, *γ* (gamma). Latin *G, g*

γῆ=ge .....*Geophilus*

When the Greek *γ* precedes *γ*, *κ*, *ξ*, or *χ*, it is transliterated as *n*.

γγ=ng ἀγγαρεία=
angaria .....*Angaria*
γχ=nc ἄγκιστρον=
ancistrum .....*Ancistrodon*
γξ=nx σφίνξ=sphinx ...*Sphinx*
γχ=nch ἄγχι=anchi ....*Anchistomum*

Greek Δ, *δ* (delta). Latin *D, d*

δάχτγλος=dactylus .....*Dactylamoeba*

Greek Ε, *ε* (epsilon). Latin *E, e*

ὑάλεος=hyaleus .....*Hyalea*

The Greek *ε* is the first letter of two Greek diphthongs:

ει=i χειλος=chilus .....*Chilostoma*
ευ=eu εὗρος=eurus .....*Eurus*
ἑ=he ἕρμαια=hermaea ..*Hermaea*
εὑ=heu εὕρημα=
heurema .....*Heurema*

Greek Ζ, *ζ* (zeta). Latin *Z, z*

ζυγόν=zygum .....*Zygocampe*

Greek Η, *η* (eta). Latin *E, e*

πειρήνη=pirene .....*Pirena*

Greek nouns ending in *η* are feminine. When transliterated, they were placed in the first Latin declension, usually the ending *-e* was used, sometimes *-a*.

λόνχη=lonche .....*Acantholonche*
χαίτη=chaeta .....*Cyclochaeta*
ἡ=he ἥλιος=helius .....*Heliactis*

Greek Θ, *θ* (theta). Latin *Th, th*

τηθύς=tethys .....*Tethys*

Greek Ι, *ι* (iota). Latin *I, i*

βαλιός=balius .....*Balia*
ἱ=hi ἵππος=hippus .....*Hippurus*

Greek Κ, *κ* (kappa). Latin *K, k*

Ἱπποκρήνη=Hippocrene ..*Hippocrene*

The Greek *κ* is sometimes incorrectly transliterated as *k*.

χεντρον=centrum .....*Kentrochona*

Greek Λ, *λ* (lambda). Latin *L, l*

λευκός=leucus .....*Leucocytozoon*

Greek Μ, *μ* (mu). Latin *M, m*

μικρός=micrus .....*Microcorax*

Greek Ν, *ν* (nu). Latin *N, n*

νέος=neus .....*Neocysta*

Greek Ξ, *ξ* (xi). Latin *X, x*

ξένος=xenus .....*Xenophora*

Greek Ο, *ο* (omicron). Latin *O, o*

ὀμφαλός=omphalus .....*Omphalocyclus*

The Greek *ο* is the first letter of two Greek diphthongs:

οι=oe οἶκος=oecus .....*Dendroeca*
ου=u λουτήριον=
luterium .....*Luterium*

In the Greek, final *-ον* usually indicates neuter nouns or adjectives. When such words were transliterated they were placed in the second Latin declension, usually with the ending *-um*, occasionally *-on*.

θηρίον=therium .....*Baluchitherium*
ἐφίππιον=ephippium ....*Ephippion*

In the Greek, final *-ος* is a nominative ending for certain nouns and adjectives. When transliterated they were placed in

the second Latin declension, usually with the ending *-us*, occasionally *-os*.

σταυρός=*staurus* .....*Tholostaurus*
τράγος=*tragos* .....*Tragos*

The ending -ος is also found in certain Greek genitives. When transliterated these words were placed in the third Latin declension, usually with the genitive ending *-is*, occasionally *-os*.

νημα, νηματος=*nema, nematis* (less correctly *nematos*) ...*Erionematis*
ὁ=*ho* ὅρμος=*hormus* ...*Hormosina*

Greek Π, π (pi). Latin *P, p*

πλατύς=*platys* .....*Platynema*

Greek Ρ, ρ (rho). Latin *R, r*

πτερόν=*pterum* .....*Pterum*
ῥ=*rh* ῥέα=*Rhea* .....*Rhea*

In composition when the second component begins with ρ and the preceding component ends in a vowel, the *r* is doubled, and the second *r* retains the *spiritus asper*.

ῥῥ=*rrh* ὀξύῤῥις=*oxyrrhis* .....*Oxyrrhis*

Greek Σ, σ, ς (sigma). Latin *S, s*

στέφανος=*stephanus* ....*Stephanastrum*

Greek Τ, τ (tau). Latin *T, t*

τέτρα-=*tetra-* .....*Tetratoma*

Greek Υ, υ (upsilon). Latin *Y, y*

μῦς=*mys* .....*Acomys*

The Greek υ is the second letter of three Greek diphthongs:

αυ=*au* γλαυκός=*glaucus* .....*Glaucus*
ευ=*eu* εὖρος=*eurus* .....*Eurus*
ου=*u* λουτηριον=*luterium* .....*Luterium*
ὑ=*hy* ὑβός=*hybus* .....*Hybolithus*
ευ=*heu* εὕρημα=*heurema* .....*Heurema*

Greek Φ, φ (phi). Latin *Ph, ph*

φύλλον=*phyllum* .....*Phyllolonche*

In a few Latin transliterations there is an alternative *ph=f*.

Greek Χ, χ (chi). Latin *Ch, ch*

χρυσός=*chrysus* .....*Chrysopyxis*

Greek Ψ, ψ (psi). Latin *Ps, ps*

Ψεῦδος=*pseudus* .....*Pseudolimax*

Greek Ω, ω (omega). Latin *O, o*

πώγων=*pogon* .....*Pogonites*

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On the Evolution and Systematics of Ciliated Protozoa

JOHN O. CORLISS

IN VIEW of the present lively interest in phylogeny of various animal groups and in application of revised concepts to the "new systematics" of such groups, it may be appropriate to consider the case of the ciliated protozoa, a fairly circumscribed assemblage of protistan forms which in recent years have been the subject of several intensive studies of considerable evolutionary significance.

Members of the entire phylum Protozoa have always presented vexing problems to the biologist seriously interested in tracing phylogenetic relationships as accurately as possible. Their microscopic size, their subcellular type of protoplasmic organization, the complete lack of fossil records among the vast majority of orders, and the common absence, today, of sexuality in many of their life cycles (a matter rather disturbing to the modern systematist with training in genetics) have proven to be obstacles of nearly insurmountable proportions. Ideas concerning degrees of kinship among the various major groups inevitably have had to be postulated almost exclusively upon the amount of similarity or dissimilarity in morphological features exhibited by present-day forms considered representative of the several groups.

Notwithstanding these obstacles, the subphylum Ciliophora probably represents the most favorable taxonomic material among the protozoa, in contrast to the less unified Mastigophora, Sarcodina, and Sporozoa, because of the very nature of the anatomical make-up of its members. In this group the major morphological characters are borne on the outside of the body proper. These pellicularly located structures have always played the leading role in over-all phylogenetic considerations of the ciliates, as has been reflected in the various classificational schemes proposed from time to time.

In the present discussion particular emphasis will be placed upon the problems of evolution and phylogenetic interrelationship at the ordinal and supra-ordinal levels. Consideration of the systematics of the lower categories, such as species, although involving some of the same general principles and certainly forming an enticing problem, would demand special treatment beyond the scope of this paper.

The Ciliophora, embracing some 5,000 [1] species which form a comparatively homogeneous and more or less isolated group of protozoa, have been the subject of considerable taxonomic study in the past. We should note, albeit briefly, the conventional bases for allocating various ciliates to several different subgroups before turning our attention to novel approaches to the problem and to the new hypotheses involved.

For nearly a century now it has been realized that the ciliates can be sorted into quite distinct groups on the basis of the topographical distribution and the structural diversification of their externally borne ciliary organelles: the simple cilia and such compound ciliary organelles as the cirri and various membranes and membranelles. The earliest sound scheme of classification, proposed by Stein in a series of classical monographs (culminating in Stein, 1867), underwent minor modification and emendation by

[1] This figure is based upon a survey of the ciliate literature, through the year 1952, just completed by the writer with the kind help of Mrs. Jura Jodele. The ranking of the orders by size, mentioned in a number of instances in later sections of this paper, is also based upon data from the same unpublished source.

his immediate successors, notably Bütschli (1887-1889), Kent (1880-1882), Delage and Hérouard (1896), and by his student Schewiakoff (1896), and some further refinement in the twentieth century, principally by Kahl (1933, 1934*a*, *b*, 1930-1935). During this period, 1867-1935, improvements were made by incorporation of new information, correction of obvious errors of fact, and more logical reinterpretations of earlier data; also considerable attention came to be paid to structures in the area of the mouth, and the possible phylogenetic value of the oral apparatus was recognized. Mention of Maupas' precise and influential work (1883) on the detailed structural anatomy of a variety of ciliates cannot be omitted. Thus, building upon the foundation established by Stein, the most easily visible structures of ciliates—their somatic and buccal ciliature—have become the principal differentiating features of use in taxonomic keys, and of weight in evolutionary considerations as well. Protozoologists in general today still adhere to these soundly established ideas, certainly not without value, concerning phylogenetic interrelationships within the Ciliophora.

New Systematics of Ciliates

What might be termed the new systematics of the ciliated protozoa does not neglect consideration of the important anatomical features mentioned above, the externally visible organelles of locomotion and feeding. The new approach to phylogenetic problems of the group, however, differs in two major respects. First, it attempts to recognize, demonstate, and then deal with, characteristics more fundamental in nature, features obviously of greater value in evolutionary studies. Secondly, it focusses attention upon study of the ontogeny [2] of various forms or, more precisely, upon morphogenetic aspects of their development during such cyclical reorganization processes as binary fission, with the conviction that such investigation provides data of sound value for the study of the phylogeny of these forms. The approach is thus actually more conservative, in spite of its newness, because of its emphasis upon more fundamental characters, yet at the same time more dynamic because of its increased attention to morphogenetic phenomena as a valuable source of evolutionary clues. Both of these aspects will receive further consideration below.

The leader in proposing the modern revision of ciliate systematics is E. Fauré-Fremiet, Professor-Emeritus of the Collège de France, Paris, an energetic man whose fifty years of intensive, precise researches in the fields of protozoology, cytology, and experimental embryology have made him particularly competent to understand the problems involved and to apply broad principles in their solution. The late Professor É. Chatton and his students must be credited for developing a nearly indispensable technique (see below) and for laying solid foundations for revised over-all taxonomic schemes in their prodigious works which involved a number of major ciliate groups. The contributions of theoretical significance made by the French schools established by both of these men will be discussed presently.

Fundamental Ciliate Characteristics

Many general features of ciliates and of their life cycles might be considered of basic systematic value within the subphylum: modes of life, feeding habits and types of nutrition (including kinds of stored food reserves), nuclear characteristics, body sizes and forms, types of symmetry, swimming patterns. (For up-to-date reviews of the great diversity among ciliates in such characteristics the reader is referred to Fauré-Fremiet, 1952, 1953*a*; von Gelei, 1950; Kahl, 1930-1935; Raabe, 1947; and current protozoological textbooks.) Difficulties arise, however, in attempting to enlist such features as these in a differential manner on a large scale.

[2] The writer cannot agree with Hadži's (1952) comment, concerning the "protista," that "In these there is no ontogeny. . . ."

The most obvious anatomical characters to employ in taxonomy are those involving the cilia or the compound ciliary organelles, as has been done in the past: the presence or absence of these organelles of locomotion and feeding and their composition, number, sizes, and topographical distribution. But one must not assume that such useful key or recognition characters, among the protozoa even as by analogy among the metazoa, are necessarily the significant ones from a phylogenetic point of view. Since any taxonomic arrangement should reflect the true evolutionary history of the groups of forms involved, the systematist must make every effort to separate obvious characteristics which may be superficial from the more conservative and more subtle ones, if the latter can be shown to be of the more fundamental significance.

Some twenty-five years ago Chatton postulated that one[8] of the most fundamental characteristics of ciliated protozoa is their universal possession of an infraciliature. The infraciliature consists essentially of the subpellicularly located basal granules or kinetosomes, which are intimately and indispensably associated with both simple and complex external ciliary systems. According to both the Chatton and Fauré-Fremiet schools, although their view has not been accepted by Klein and certain other workers (see esp. Klein, 1933, 1943), the argentophilic kinetosomes, the principal elements of the infraciliature, are autonomous, self-duplicating, ever-present cytoplasmic organelles endowed with genetic continuity. Thus the infraciliature as an anatomical feature alone appears very serviceable as a fundamental, conservative, systematic character. Its role in morphogenetic phenomena, likewise of great potential value in evolutionary considerations, will be discussed in the following section.

Also located subpellicularly as a part of the somatic infraciliature of many ciliates are fibrillar structures of some sort. These fibrils, known as the kinetodesmas, are associated with the kinetosomes (see p. 74 for brief discussion of this relationship), forming with them the so-called kineties, structures which also are said to exhibit autonomy and genetic continuity.

The infraciliature obviously possesses a greater value in systematics than does the superficially located somatic and buccal ciliature. The subpellicularly located kinetosomes are more conservative, typically exhibit neither hypertelic development nor secondary regression, and, most important of all, are as a rule never absent from any phase in the life cycle of the organism. In encystment, regeneration, and various other protoplasmic reorganizational periods in the life history, often including binary fission itself, the locomotor and feeding organelles may be dedifferentiated or resorbed; the infraciliary counterparts of these same organelles, however, persist, as may be seen with proper techniques.

What may be considered particularly significant from an evolutionary point of view has been the discovery of the existence (or better, persistence) of kinetosomes in mature forms which are quite devoid of external ciliature: such revelations, carried out in certain members of the SUCTORIDA, the TRICHOSTOMATIDA, and the THIGMOTRICHIDA, for example, have supported beautifully the theory of genetic continuity of the infraciliature throughout ontogeny. The larval stages in these cases do possess an external ciliature; but it has been produced by the segment of parental infraciliature which has been passed on to the filial generation during the budding process.

Value of Morphogenetic Data

As has long been known, in systematic study of ciliates as well as of other protozoa and of metazoa, too, examination of

[8] The primary concern of the present paper is not with characteristics which distinguish ciliates from other protozoa (nuclear makeup, mode of division, etc.; see p. 80) but rather with features which allow discussion of the evolutionary diversity which presumably has occurred within the Ciliophora.

stages in the ontogenetical cycle from one mature form to the next may provide valuable clues regarding ancestral relationships. The mechanisms underlying the morphogenetic phenomena inevitably involved in such cycles are of great interest to biologists in general, but studies of these processes also supply information which can be considered of special significance to the systematist. It is this kind of information only to which we must limit our attention in the present paper. For references to major works on ciliate morphogenesis *per se*, the reader is referred to the recent comprehensive reviews by Lwoff (1950), Fauré-Fremiet (1948*a*, 1954*b*), Weisz (1954).

Following the discovery and recognition of an ever-present infraciliature as a most fundamental feature of ciliates, and armed with a technique with which it can be demonstrated with comparative ease in all stages of the life cycle (see below), it has been possible to study the roles of the infraciliary counterparts of the somatic and the buccal ciliature during such major morphogenetic processes as binary fission and stomatogenesis. When investigations are carried out on a comparative basis, or at least are so analyzable later, the data obtained often may be of great aid in postulating taxonomic affinities of the groups involved. Three instances of this are mentioned briefly here in illustration of the point; more cases will be cited under appropriate ordinal headings in later sections below.

(1) Study of the infraciliature during the dynamic endogenous budding process of certain of the SUCTORIDA reveals not only that the mature parental organism possesses kinetosomes (erratically arranged and without cilia) but also that the external ciliature of the migratory larval form arises from basal granules passed on to it in an orderly fashion from the parental organism. This occurs during the complex morphogenetic phenomenon of fission (see Pl. I, Fig. 3). When the aligned infraciliature of the free-swimming stage is compared with the infraciliature demonstrable in numerous species belonging to long-recognized holotrichous orders in good standing, it becomes apparent that the suctoria show a closer kinship with such orders than formerly believed.

(2) Re-examination of binary fission in certain highly evolved trichostomes which divide within a cystic membrane, with techniques revealing the pattern of the infraciliature, supports nicely the hypothesis that simplification of the body form and return to a single axis of symmetry, plus dedifferentiation of the ciliary organelles in general, indicate an ancestral origin of the true TRICHOSTOMATIDA from a ciliate not unlike certain of the more primitive GYMNOSTOMATIDA known today (see Pl. I, Fig. 2). Such gymnostomes have been shown to exhibit the same sort of morphogenesis during fission while not showing in their ontogenetical cycles the more complex mature stages characteristic of these highly asymmetrical trichostomes.

(3) Investigations of stomatogenesis (see Pl. I, Fig. 1), a developmental process which has served as a beautiful example of an implicit morphogenetic phenomenon in studies of "embryology at the protozoan level," reveal that the infraciliary make-up and mode of duplication of the buccal apparatus show striking parallels among various of the ciliophoran orders. Coupled with other data, such facts aid greatly in postulating the origin of certain more highly evolved groups from allegedly more primitive ones, such as the peritrichs and the thigmotrichs from the hymenostomes, or even more striking, the spirotrichous heterotrichs from the holotrichous hymenostomes.

The Silver Impregnation Technique

Allusion has been made several times in preceding sections to a cytological technique ideal for revelation of the somatic and buccal infraciliature. To the Austrian protozoologist Bruno M. Klein should go full credit for discovery of a

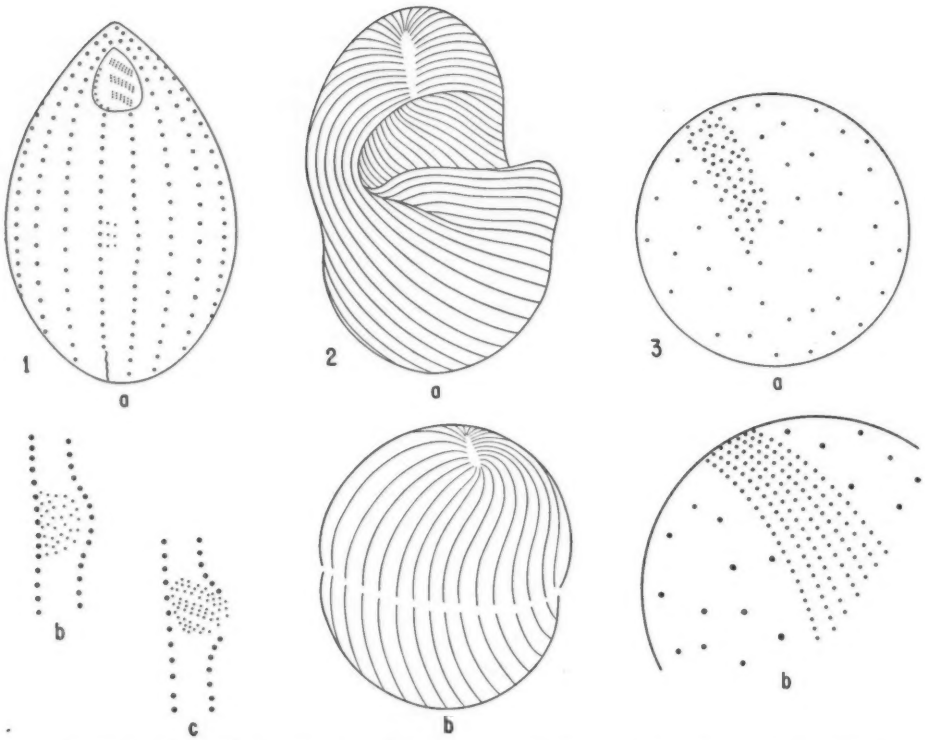

PLATE I. Anatomical features and morphogenetic phenomena of importance in the new systematics of ciliated protozoa. All diagrammatic representations. FIG. 1. Infraciliature and stomatogenesis in the hymenostome *Tetrahymena*. (Based on figures in Corliss, 1953*b*.) (*a*) Ciliate in ventral view showing subpellicularly located argentophilic basal granules or kinetosomes of both somatic (longitudinal rows) and buccal (bases of UM and AZM) infraciliature. Kinetodesmal fibrils have been omitted. Note the few granules out of line in the mid-ventral, subequatorial area of the body; these have been produced by the so-called stomatogenous meridian or kinety "number 1," the ciliary row which also, posteriorly, bears the cytoproct. (*b*) Later stage in stomatogenesis, enlarged, showing only the area of presumptive mouth region of the posterior daughter (*opisthe*), in which an anarchic field of basal granules has now developed just to the left of the stomatogenous kinety as the *anlagen* of new buccal organelles. (*c*) Still later stage. The granules have become oriented and organized as bases of the definitive AZM and UM; during subsequent morphogenetic movements these bases will become located in the fully formed buccal cavity of the *opisthe*. FIG. 2. Reorganization in binary fission of the trichostome *Tillina*. (Based on figures in Corliss, 1953*b*; from Tuffrau, 1952.) (*a*) Mature, free-swimming stage. Lines represent the pattern of ciliary meridians or kineties; the individual argentophilic basal granules composing them have not been depicted. Broad depressed area is the vestibulum; mouth is out of sight. Note complexity of body form reflected in the pattern of the organism's somatic infraciliature. (*b*) Fission within a cyst (membrane not shown), following extensive dedifferentiation of pellicular structures, loss of mouth, and simplification of body axis. Body form and mode of division now recapitulate ancestral conditions, as still found among primitive gymnostomes. Redifferentiation to produce excysted mature forms again will involve stomatogenesis and marked morphogenetic movements including allometric growth of dorsal kineties. FIG. 3. Infraciliature in the suctorian *Podophrya* at early stages in the phenomenon of reproduction by budding. (Based on figures in Chatton *et al.*, 1929.) (*a*) Here may be seen the erratic distribution of argentophilic kinetosomes, which bear no cilia, typical of the mature adult organism, but note the area in which multiplication of granules has now taken place. (*b*) Enlargement of the embryonic field region of the parental body, in a slightly later stage, showing alignment of the kinetosomes which will produce the external ciliature of the holotrichous larval form. For the relationship between mature and budding forms in a much later stage see Plate III, Figure 6 (different species but probably same genus).

simple yet ingenious modification of the well-known histological method of silver impregnation of unique value in investigations of the pellicular and subpellicular anatomy of ciliates. This opened the way to an entirely new approach in comparative morphological studies of these protozoa. For some fifteen years, commencing in 1926, Klein subjected scores of species to the silver treatment and published dozens of important papers on the *Silberlinien-* or *neuroformative*) *System* of these forms (see Klein, 1926*a*,*b*, and bibliography in Klein, 1943). He early recognized the potential value of the silverline system in systematics, for it soon became apparent that each species possesses a stable, characteristic pattern of argentophilic structures, notably the basal granules or kinetosomes, and that members of closely related genera are more alike than members of distantly related groups, etc.; the Austrian worker himself, however, was generally not concerned with tracing phylogenetic relationships.

Various modifications and refinements of the original dry technique of Klein have arisen: principal alternative methods include those developed by von Gelei and Horváth in Hungary, by Chatton and Lwoff in France, and, more recently, by Fernández-Galiano (actually a modification of Rio Hortéga's piridinated silver carbonate histological method) in Spain, and by Kirby (using Bodian activated protein silver) in America.

The monumental works of the schools of Chatton and Fauré-Fremiet (see following sections) on which one must rely heavily for up-to-date information of importance in the new systematics of ciliates, have all made use of the French technique, with which the present writer is also most familiar (Chatton and Lwoff, 1930; and see Corliss, 1953*a*). The three outstanding advantages of this silver method over the rather drastic dry technique of Klein's, in which the animals are fixed by exposure to air until dried before application of the silver nitrate solution, are these: the ciliates are preliminarily fixed with an osmic acid fixative and, later, they are embedded in a layer of gelatin. These two procedures guarantee preservation of the natural form of the body and allow impregnation of all surfaces, both requisite conditions for investigations of the fate of the argentophilic infraciliature during morphogenetic phenomena. Thirdly, the technique, unlike Klein's, works equally as well with marine and symbiotic species, in all stages of their life cycles, as it does with free-living, fresh-water forms.

The silver impregnation method is not unique in its revelation of ciliate infraciliature; basal granules were seen and well described many years before Klein and Chatton and Lwoff. Nevertheless the technique seems unsurpassable as a standard way of consistently revealing bases of both the entire somatic and buccal ciliature in whole mounts of organisms in various stages of their complete life cycles.

Pertinent Investigations and Hypotheses

Forming the foundation of any taxonomic arrangement are the scores of descriptive works, large and small, heralded or practically unnoticed, concerned with the hundreds of species comprising the groups in question. Combine this indispensable, detailed wealth of analytical information with some theoretical considerations (syntheses) of an evolutionary nature, and a classificational scheme of some phylogenetic value emerges. This has been true in the past history of the ciliated protozoa, and often the men providing the greatest quantities of descriptive data have also been responsible for promulgation of the most significant theories: the names of Stein, Bütschli, and Kahl, at least, should be cited as outstanding examples of this. Protozoology's debt to such men can never be overestimated.

It may be asked justifiably, then, why or how is it possible all of a sudden, as it were, to be able to suggest major re-

visions in a systematic arrangement already so well and seemingly soundly established? As already emphasized earlier, many of the new data now available are important, actually out of proportion, because they are of a different kind, involving as they do the infraciliature. This universal property of ciliates was generally unrecognized, at least in its full significance, as recently as a quarter of a century or less ago. And the new hypotheses which have arisen are also different, and often more precise, because of their close dependence upon the existence of this infraciliature alone and/or its dynamic role in morphogenesis. Thus at this point we should consider, even though very briefly, the major investigations and the most important ideas of the two French schools to which reference has been made earlier. For it is clear that to date it has been almost exclusively the analyses and syntheses of Chatton and Fauré-Fremiet, and their associates, which have made possible the modern revisions in the over-all systematic picture of the subphylum Ciliophora.

Contributions of Chatton. The beautiful productions of the Chatton school (composed, as far as ciliated protozoa were concerned, principally of É. and M. Chatton, A. and M. Lwoff, Mlle. Séguéla, and Mme. Villeneuve-Brachon) have been very significant in ciliate systematics in three main ways: in revelation of the infraciliary anatomy and its role in morphogenesis in a wide variety of ciliates, employing the refined silver impregnation technique; in establishment of certain entire orders on a sound taxonomic basis, viz., the APOSTOMATIDA and the THIGMOTRICHIDA (see following sections under these ordinal headings); and in promulgation of certain hypotheses of great theoretical value. Among their theories, principally to be credited jointly to Chatton and his most able and most prolific student, André Lwoff, the following are the ones of greatest pertinence for the general subject under consideration in the present paper:

(1) The hypothesis of the autonomy and genetic continuity of the infraciliature, particularly of the argentophilic ciliary basal granule or kinetosome. This was postulated after its validity was demonstrated in a wide variety of forms, including representatives of several orders in which external ciliature is absent from some major stage in the life cycle. To the writer's knowledge no indisputable refutation of this most fundamental idea, of such tremendous importance in both systematic and morphogenetic problems, exists. (The curious case of *Cyathodinium*, in which new somatic ciliature appears to be derived from a completely endoplasmic vacuole during the processes of fission and reorganization (Lucas, 1932; Nie, 1950), remains enigmatic; reexamination of this problem employing a silver technique might prove to be highly profitable.)

(2) The pluripotency of the kinetosome in morphogenetic phenomena, including its role in stomatogenesis. Basic patterns of new mouth formation (i.e., the origin and development of the new mouth parts, the buccal organelles) were postulated after precise examination of the phenomenon in representative ciliate orders. The concept of the duality of the basal granule-complex may be listed here, too.

(3) Various roles of the ciliary meridians or kineties in fission, involving the phenomena of growth by elongation, elineation, etc. The concepts of homothetigeny and symmetrigeny also may be included here: these ideas, involving so-called perkinetal and interkinetal types of division, contrast the modes of fission characteristic of ciliates, on the one hand, and flagellates (including opalinids) on the other (see brief explanation and reference to the original literature in Corliss, 1955*a*). A large number of exceptions actually exist to this generalized rule of *scission percinétienne* for ciliates: witness the cases of reproduction by budding or by very unequal binary fission in which organized kineties are not directly or equally transected; also the cases, including many of the spirotrichs, in which practically no somatic ciliature or infra

ciliature exists. Often, however, proper morphogenetic movements come into play to provide finally a pair of filial organisms which are in a homothetic relation to each other. But there is definitely no genetic continuity of organized, longitudinal kineties, as such, in the interesting case of the hymenostome *Ichthyophthirius multifiliis,* as revealed in a precise investigation by Mugard (1948).

(4) The role of erratic kinetosomes. The belief that certain basal granules belonging to the disorganized somatic infraciliature characteristic of many ciliates play a vital role in the genetic continuity of structures in these forms has been a most important contribution to our understanding of morphogenetic processes in species belonging to such orders as SUCTORIDA, THIGMOTRICHIDA, HETEROTRICHIDA, and HYPOTRICHIDA. In turn such newly gained information may be utilized in considerations of phylogeny and evolution, as we shall see later in appropriate sections of the present paper.

(5) The rule of desmodexy. This important hypothesis maintains that linearly arranged kinetosomes are always accompanied by a fine fibril, generally argentophobic, with which the basal granules are intimately associated in some way, and that this kinetodesma invariably lies to the (animal's) right of the row of kinetosomes. This endows the whole ciliary meridian or kinety (granules+fibril) with an asymmetry and thus with anteroposterior polarity; furthermore, the whole organism now becomes endowed with the same polarity since the kineties are, ideally, longitudinally arranged, independent structures coursing the entire length of the ciliate (except for the postoral meridians).

The writer takes exception to the implied universality of this rule, since a number of forms apparently do not possess kinetodesmas. Obviously species without orderly arranged somatic kinetosomes are not likely to have such structures: many spirotrichous and some holotrichous groups fall into this category. Even in larval forms of the SUCTORIDA, where simple holotrichous ciliature has been demonstrated (Guilcher, 1951), the unifying fibril, the kinetodesma, is absent. Its presence is either denied or it has not been revealed convincingly in scattered cases among both lower and higher gymostomes, the chonotrichs, the trichostomes, and the peritrichs. This is one of the areas of study in which more information is sorely needed. Further work with the electron microscope should furnish valuable data: neat corroboration of the law of desmodexy has been provided in research of such kind published to date, but this has involved only two genera of hymenostome ciliates, forms in which it was not surprising to find a kinetodesma (Metz and others, 1953; Metz and Westfall, 1954; Sedar and Porter, 1955).

(6) Various generalizations concerning evolutionary pathways, termed "orthogenetic lines" by the French, within certain families and orders, particularly groups exhibiting symbiotic modes of life. Some of these will be cited in following sections of this paper concerned with the appropriate order. One might include here Chatton's view concerning the derivation of "circular ciliature," believed by him to be present in the PERITRICHIDA, from meridional ciliature.

Contributions of Fauré-Fremiet. The contributions of Fauré-Fremiet and, in relatively recent years, of his protozoologically minded students, most notably Mlle. Mugard (Mme. Dupré) and Mlle. Guilcher (Mme. Škreb), likewise have been of great significance to ciliate systematics in sheer amount of original descriptive data and in theoretical propositions related to evolutionary problems. And from his profound interest in cytological ultrastructure, on the one hand, and his passion for investigation of the kinetics of growth and differentiation, on the other, Fauré-Fremiet has become a recognized leader in the whole field of morphogenesis; for us here his researches on the mechanisms of morphogenesis in ciliates are most pertinent. The major

theoretical contributions of the Fauré-Fremiet school to the new systematics of the Ciliophora may be discussed briefly, leaving to one side mention of his concepts in the field of senescence and rejuvenescence in ciliates and his impressive output of precise investigations of purely descriptive or ecological nature:

(1) Extension and amplification of an hypothesis originally proposed by Furgason (1940). The American worker had identified part of the buccal ciliature in the hymenostome genus *Tetrahymena* as representing a primitive but true adoral zone of membranelles (AZM), always conventionally considered absent in holotrichs, postulating it to be completely homologous with the well known prominent AZM of such highly evolved spirotrichous forms as the hypotrichs. The undulating membrane (UM) of holotrichs was also considered to be homologous with the similarly located UM of spirotrichs. Furgason suggested, furthermore, that this fundamental buccal pattern (three membranelles composing the AZM, on the left, plus one paroral or undulating membrane, on the right) might be found widespread among holotrichs. The idea lay dormant until Fauré-Fremiet realized and extended its great evolutionary possibilities. With Mlle. Mugard, in particular, he set out to demonstrate the presence of an AZM (and UM) in a wide variety of hymenostomes. Following clarification of homologies within this order he showed the probability of widespread involvement of the basic tetrahymenal buccal organization in evolution of other entire groups. This leads smoothly into the following, related contribution.

(2) Reinterpretation of data supplied in the works of Chatton and Lwoff. To fulfill his expanded revision of the Furgason hypothesis, Fauré-Fremiet found it possible and very expedient to reconsider the exact identity of buccal structures in forms described by his fellow countrymen; the THIGMOTRICHIDA and PERITRICHIDA were particularly involved. This has allowed him to establish the important evolutionary line: hymenostomes → thigmotrichs → peritrichs, in addition to postulation of a hymenostome → heterotrich sequence. The evidences behind these proposals will be considered to some extent under the appropriate ordinal headings in following sections.

(3) Analyses of mechanisms of morphogenesis, particularly the roles of ciliary fields in fission and of buccal *anlagen* in stomatogenesis. His ideas concerning modes of stomatogenesis and the evolutionary trend towards autonomization of the ciliary buccal system are of value to the systematist as well as to the experimental biologist. He was the first to recognize and name the enantiotropic fission characteristic of the OLIGOTRICHIDA: this type of division involves a condition of inverse homothety, whereas the fission typical of most ciliates exhibits direct homothety (homiotropic fission). Also one could include here Fauré-Fremiet's concepts concerning the involved morphogenetic movements in fission and regeneration, the allometric growth of localized kineties, the regeneration of kinetal segments, and the morphogenetics of ontogeny in general.

(4) Contributions towards a better understanding of such fundamental matters as symmetry, polarity, axial relationships, the dynamic processes of regulation, force-structure relationships, macromolecular composition of cytoplasmic structures. Most of these works have been of an experimental nature, being a kind of experimental embryology at the protozoan level.

(5) Ideas concerning life cycles and polymorphism, relationship of migratory to sedentary forms in various orders, development of organelles of attachment, phylogenetic significance of the scopula of the PERITRICHIDA. Some of his thinking along these lines was carried out over fifty years ago; some in more recent years, in which work the Chatton-Lwoff silver impregnation technique was employed. Unlike Chatton, Fauré-Fremiet has been concerned primarily with free-

living, and commonly fresh-water, ciliates.

(6) Finally, his most recent postulations regarding the evolutionary relationship among the various major orders of ciliates. These, based upon his own long years of observation and upon a comprehensive knowledge of the work of others, have resulted in his revision of the classical scheme of ciliate classification and in his construction of a new phylogenetic tree. This has been summarized in a rather brief paper published several years ago (Fauré-Fremiet, 1950*a*).

Arrangement in Present Paper

The systematic arrangement of ciliate orders suggested in the present paper is based primarily upon that given in Fauré-Fremiet's brief but important 1950 publication. The writer is, in general, in full accord with the taxonomic innovations proposed there by Fauré-Fremiet. From the basic outline he has furnished one may construct a fuller picture. In review and expansion of his scheme an effort is made here to include pertinent data, critically analyzed, published by a number of workers since 1950, and certain orders which were left to one side by Fauré-Fremiet are considered in sufficient detail to complete the over-all systematic picture.

The writer's own ideas concerning homologies of buccal structures and of somatic areas in the vicinity of the oral apparatus throughout the subphylum, as yet unpublished in full, are incorporated in the present treatment but not in detail; fuller presentation would be beyond the scope of this paper.

Minor refinements of a nomenclatural nature have been made throughout, such as application of quite rigid uniformity in the formation of the stem and endings of ordinal and subordinal names. In the spirit of the Copenhagen Decisions on Zoological Nomenclature regarding higher categories (Hemming, 1953, pp. 38-43), genera more or less taxonomically central to the collection of subunits involved will be mentioned in connection with each order or with its suborders. The writer is not presuming, however, to designate here single, specific type genera for all of these higher groups, but generally is suggesting representative genera, often several in number, from which types, if needed, might be selected at a more appropriate time and place.

The emphasis in the presentation of ciliate systematics being made here is not on the originality of the scheme, for the arrangement is essentially that of Fauré-Fremiet, nor does the paper represent any attempt to offer complete taxonomic descriptions of the various taxa, with lists of included species, etc. Rather the plan for the rest of this account is to show how application of the new hypotheses just described, themselves based primarily upon new data obtained with new techniques, will permit and justify a revised scheme of classification, a scheme which, in the writer's opinion, reflects the phylogeny and evolution of the Ciliophora in perhaps a more natural way than do other current arrangements. Certain aspects of the over-all problem have been considered in a preliminary way in earlier papers by the writer (Corliss, 1953*b*, 1955 *a*, *b*, *c*).

Areas of Major Revision

Before turning to factors important in the new systematics of each order, we should consider briefly the major areas in the hierarchy of ciliophoran forms which have been subjected to most significant revision. The groups marked with an asterisk in the left and center columns of Table I are those bodily shifted about or excluded entirely from the subphylum, as may be noted by comparison with the list comprising the column on the right.

The class, or subclass, according to most extant schemes, Protociliata is banished from the subphylum Ciliophora *in toto*. This controversial move has been discussed in some detail quite recently [4]

[4] Reference inadvertently was omitted there to the stimulating ideas of Ulrich (1950) who similarly places the opalinids in a position quite separate from the ciliates. Naming them the "Ciliatoidea," Ulrich considers these

TABLE I—CLASSIFICATION SCHEMES FOR THE PROTOZOAN SUBPHYLUM CILIOPHORA

1. CONVENTIONAL MODERN SCHEMES*		2. PROPOSED NEW SCHEME
A. AFTER DOFLEIN AND REICHENOW (1949–1953)†	B. AFTER JAHN AND JAHN (1949) AND HALL (1953)	(FROM CORLISS, 1955*b*, AND ESSENTIALLY FAURÉ-FREMIET, 1950*a*)
Class I. *Protociliata Fam. *Opalinidae	Class I. Ciliatea Subclass *1.* *Protociliatia Order 1. *OPALINIDA	Class I. Ciliata Subclass *1.* Holotricha Order 1. GYMNOSTOMATIDA
Class II. Euciliata Order 1. HOLOTRICHA Suborder (1) Gymnostomata Tribe *1.* Prostomata *2.* Pleurostomata *3.* Hyposto-mata (2) Trichostomata (3) Apostomea (4) Hymenostomata (5) Thigmotricha *1.* Stomodea *2.* Rhynchodea (6) Astomata 2. SPIROTRICHA (1) Heterotricha (2) Oligotricha (3) Entodiniomorpha (4) Ctenostomata (5) Hypotricha 3. *PERITRICHA (1) Mobilia (2) Sessilia 4. *CHONOTRICHA 5. *SUCTORIA	Subclass *2.* Euciliatia Order 1. HOLOTRICHIDA Suborder (1) Gymnostomina Tribe *1.* Protostomata *2.* Pleurostomata *3.* Hyposto-mata (2) Trichostomina (3) Hymenostomina (4) Thigmotrichina (5) Apostomina (6) Astomina 2. SPIROTRICHIDA (1) Heterotrichina (2) Oligotrichina (3) Tintinnina (4) Entodiniomorphina (5) Hypotrichina (6) Ctenostomina 3. *PERITRICHIDA (1) Mobilina (2) Sessilina 4. *CHONOTRICHIDA Class II. *Suctorea	2. SUCTORIDA 3. CHONOTRICHIDA 4. TRICHOSTOMATIDA 5. HYMENOSTOMATIDA (1) Tetrahymenina (2) Peniculina (3) Pleuronematina 6. ASTOMATIDA 7. APOSTOMATIDA 8. THIGMOTRICHIDA (1) Stomatina (2) Rhynchodina 9. PERITRICHIDA (1) Sessilina (2) Mobilina Subclass *2.* Spirotricha Order 1. HETEROTRICHIDA 2. OLIGOTRICHIDA 3. TINTINNIDA 4. ENTODINIOMORPHIDA 5. CTENOSTOMATIDA 6. HYPOTRICHIDA

* The groups marked with an asterisk are those subjected to the greatest changes in position in the proposed scheme presented in the third column above; note that the "Protociliata" are excluded entirely from the hierarchy of ciliated protozoa.

† The scheme in Kudo (1954) is very similar although his assignment of subclass rank to the "protociliates" and his consideration of the Suctoria as comprising a class, rather than an order, follow Doflein and Reichenow (1927–1929); in these respects the system presented in the center column above also follows the earlier edition of the German treatise.

(Corliss, 1955*a*) and need be mentioned here only very briefly. The opalinids are highly differentiated, highly evolved forms, not likely ancestral to any other group of existing protozoa. Their alleged symmetrigenic mode of binary fission, their exhibition of a strictly monomorphic nuclear apparatus, and their possession of a reproductive cycle involving true syngamy between anisogamous gametes would appear to link them strongly with

"cilia-clad" protistan forms with but a single kind of nucleus to hold a rank equivalent to the Mastigophora, Rhizopoda, and Sporozoa (*s. str.*) within a subkingdom *Cytomorpha*, the Ciliophora alone occupying a second subkingdom *Cytoidea* (italicized names after Hatschek). In their table of "The Phyla and Classes of Animals," Mayr *et al.* (1953; p. 54) also separate the opalinids from the ciliates, without comment, and reveal that they have been strongly influenced by Ulrich's arrangement in their listing of the other protozoan groups as well.

flagellates in general. Their mouthless condition, symbiotic (saprozoic) existence, geographical distribution, body size and form, possession of numerous fine locomotor organelles, seemingly acentric mitosis, and other such characters, may be considered to be of little real differential value at the higher levels; some of them are very likely of a secondarily derived nature, and others may have come to resemble characteristics typical of other groups by convergence through millions of years of parallel evolution. If the category "Protociliata," with all its misleading connotations, is dropped, then there is no longer need for retention of the term "Euciliata" for the true ciliates.

The changes whereby most of the suborders in conventional systems become orders in the new scheme might appear to be a move only of nomenclatural expediency. Actually, however, this shift has been made to emphasize, on the one hand, the distinctiveness and individuality of the groups and, on the other hand, to show in more proper perspective the levels of interrelationship among all fifteen ciliophoran orders.

The retention in the subphylum of a single class, the Ciliata, will appear unnecessary to some protozoologists. If one holds, however, that the entire subphylum comprises a fairly homogeneous, closely-knit group of forms, then this may be indicated by separation of the holotrichous and spirotrichous assemblages at a level below the rank of class. This appears important to the writer when the breakdown of all four protozoan subphyla is considered in a comparative way. The two subclasses Holotricha and Spirotricha thus compose the single class.

Among the most controversial changes are those involving the enigmatic groups conventionally considered as representing very distinct categories among the ciliates: the peritrichous, chonotrichous, and suctorian groups. Their incorporation into the holotrichous fold will be defended in reasons offered under appropriate ordinal sections, below. Subordination of the suctoria to a rank among the Holotricha equivalent to the gymnostomes, hymenostomes, etc., represents a shift of even greater proportions than is indicated by comparative study of the first and third columns in Table I, since the group generally is still separated from all other ciliates at the class level, as may be seen in the center column (also see Doflein and Reichenow, 1927–1929; Calkins, 1933; Jírovec *et al.*, 1953; Kudo, 1954). Hall was appreciative of the ideas of Fauré-Fremiet (1950*a*), however, and predicted (Hall, 1953, footnote p. 333) that "the older system" of ciliate classification may come to be replaced by revisions of the type suggested by Fauré-Fremiet, acknowledging that "rapidly accumulating data tend to support these proposals."

Some changes are not apparent at all in the parallel listings of taxa in Table I. Frequently, by coincidence, the arrangement of groups, presumably indicating degrees of phylogenetic relationship, is identical in all columns. But the basis for the reflected evolutionary affinities may be different, often being founded upon fuller use and new interpretation of major modern taxonomic works which place the proposed kinship on firmer ground than before.

Problem of Uniform Endings

The use of uniform endings for protozoan taxa at suprafamilial levels is not original with the writer. In the list of zoological names prepared for Section F of the AAAS some twenty years ago, Pearse (1936), as editor, published an "alternative list" of nomenclature employing rigid uniformity in choice of suffixes. As far as the protozoa were concerned, this move apparently had the blessings of a representative group of American protozoologists, headed by L. E. Noland, who had been consulted. Pearse wrote, "In presenting this report . . . it is not supposed that uniform endings shall be adopted as official, or even recommended . . . perhaps . . . the editor is 'a hundred years ahead of his time.' " And in subsequent editions (e.g., Pearse, 1949) the column of names with uniform endings was

dropped from the report. For the protozoa the matter has been reopened by the resurrection of uniformity in endings in the recently published books by Jahn and Jahn (1949) and Hall (1953): note the center column in Table I. (Actually in the often overlooked work by Delage and Hérouard, 1896, not only were uniform endings employed for the several higher categories but the four orders recognized among the ciliates were written with *-ida* suffixes as follows: HOLOTRICHIDA, HETEROTRICHIDA, HYPOTRICHIDA, PERITRICHIDA.)

It is beyond the scope of the present paper to discuss the pro's and con's of such taxonomic innovations for the protozoa or for animal groups in general; the subject has been expounded upon quite recently in pages of this journal by several zoologists. The writer has followed a middle course here in supporting vigorously the adoption of *-ida* and *-ina* suffixes for the ordinal and subordinal taxa of protozoa but ignoring the suggested endings of *-ea* and *-ia* in class and subclass nomenclature. The reasons for this, briefly, are that whereas the ordinal groups are, as a rule, the most stable and conservative taxa in the phylum Protozoa and thus most logically should be set up on a consistent plan of terminology, the higher categories, fewer in number and even more subjective in nature, have been and may well continue to be more susceptible to changes of raising or lowering. Rigid application of uniform endings for these higher levels, then, would cause constant shifting from *-ea* to *-ia* and/or back again, depending upon the author, and bring about unnecessary confusion in the literature and undesirable hardship on students of the groups concerned.

In the following accounts, for all taxa above family rank, names of the authorities who first proposed the names for the general groups of ciliates in question are furnished, accompanied by dates, for the sake of completeness and to give full credit to the proper workers involved. The writer does not subscribe to the notion that a name should be considered new because of a slight change in spelling, a shift in its rank, or even a change in conception of the exact boundaries of the group it represents. As mentioned above (p. 76), names of genera considered representative by the writer are supplied for each order or suborder included in the following brief systematic treatment of the subphylum. Throughout the paper ordinal names only always will be written in capital letters.

The nomenclatural histories of the higher taxa treated in the present work often are long and confused and are in serious need of review. Space will not permit adequate discussion here of any of the legalistic problems involved; a separate paper on the subject is being prepared for publication elsewhere.

Subphylum Ciliophora Doflein, 1901

For the sake of proper orientation it may be mentioned briefly that this entire group is set apart from all other protozoa principally on the following bases:

(1) Its universal possession of a subpellicularly located, autonomous infraciliature so important in comparative morphology within the subphylum and so vital in morphogenetic phenomena.

(2) Its homothetigenic mode of division (which is strictly perkinetal in nature, however, only among the less highly differentiated forms).

(3) Its exhibition of nuclear dimorphism; i.e., its possession of differentiated micro- and macronuclei, the former undergoing presumed acentric mitoses.

(4) Its lack, in carefully confirmed studies of present-day forms, at least, of a sexual reproductive cycle involving fusion of true gametes.

(5) Its greater morphological complexity in externally located structures, such as the highly differentiated organelles of locomotion and feeding; and its diversity in development of organelles of attachment, food storage, etc., in forms which have adopted symbiotic modes of life (Kirby, 1941; Raabe, 1947).

Class I. Ciliata Perty, 1852

Characteristics of the subphylum, since this is the only class included. Existence of a single class points up the homogeneity of the entire group which truly seems to have had a monophyletic origin somewhere in the unknown past.

Subclass 1. Holotricha Stein, 1859

Primitively and fundamentally this group may be considered to have been composed of forms with quite uniform ciliation, often covering the entire body, with simple axes of symmetry, and with complete lack of more highly specialized, compound ciliary organelles. In many orders included here these conditions appear to have persisted, at least in some stage of the life history.

The characterization persisting even in the most modern textbooks, however, that the holotrichs are completely "without an adoral zone of membranelles," is inaccurate if one agrees with Furgason, Fauré-Fremiet, and others (see p. 75), that a primitive but true AZM does occur in this subclass. An extensively developed AZM is commonly lacking, however, except in the order PERITRICHIDA; even here, where it is prominent, it is presumably not composed in the same manner as in the spirotrichs (see section on peritrichs, below). Typically absent from all included orders are the compound ciliary organelles known as cirri.

Thus there are both general and specific indications, supported by numerous examples and universally accepted by protozoologists, that the holotrichous ciliates as a group are simpler and less highly differentiated than the spirotrichs and very likely preceded them directly in the evolutionary timetable of protistan forms.

Order 1. GYMNOSTOMATIDA Bütschli, 1889

A large order embracing a great variety of forms, many of quite large size and of common occurrence in nature; in actual number of species it ranks third in the subphylum, trailing the peritrichs and the tintinnids. When symmetry, structural simplicity, and the morphogenetic mechanisms of fission and of stomatogenesis are carefully considered, it appears logical to place the gymnostomes at the base of the ciliate genealogical tree. The most primitive forms, with their apically located cytostome, simple axis of symmetry, and uniform somatic ciliature, may well be considered the prototype of the Ciliophora (see Pl. II, Fig. 1). The popular belief that the ASTOMATIDA, by virtue of being mouthless, are the "first" ciliates seems untenable: mouths could be lost secondarily in forms living saprozoically. There is other evidence, too, that the astomes may represent degenerate lines, perhaps having origin in several different orders; for discussion of this problem see the section on the "order" of astomes, below.

The long standing and conventional subdivision of the GYMNOSTOMATIDA into three "tribes" on the basis of mouth location may be considered less accurate in portraying phylogenetic interrelationships than dividing the entire group into only two sections on the basis of their cytopharyngeal [5] structures. The "prostomes" and the "pleurostomes" of the

[5] Attempts to recognize homologies in structures or areas associated with ciliate mouths become of crucial importance in revising the systematics of the Ciliophora; and terminology as uniform as possible should be employed. Five terms—*cytostome* (the true mouth), *cytopharynx*, *vestibulum* (bearing vestibular, really more or less modified somatic, ciliature), *buccal overture*, and *buccal* or *peristomial cavity* (wherein are found the bases of the compound ciliary organelles known as the *AZM, adoral zone of membranelles*, and the *UM, undulating membrane*, or their alleged homologues)—are considered by the writer to be sufficient for the areas involved in species of all fifteen orders, although diverse terminology and conflicting definitions abound in the literature. The terms are used throughout the present work in accordance with descriptions and definitions offered briefly elsewhere by the writer (see esp. Corliss, 1955*c*); the matter will receive detailed attention as subject of a future, separate paper.

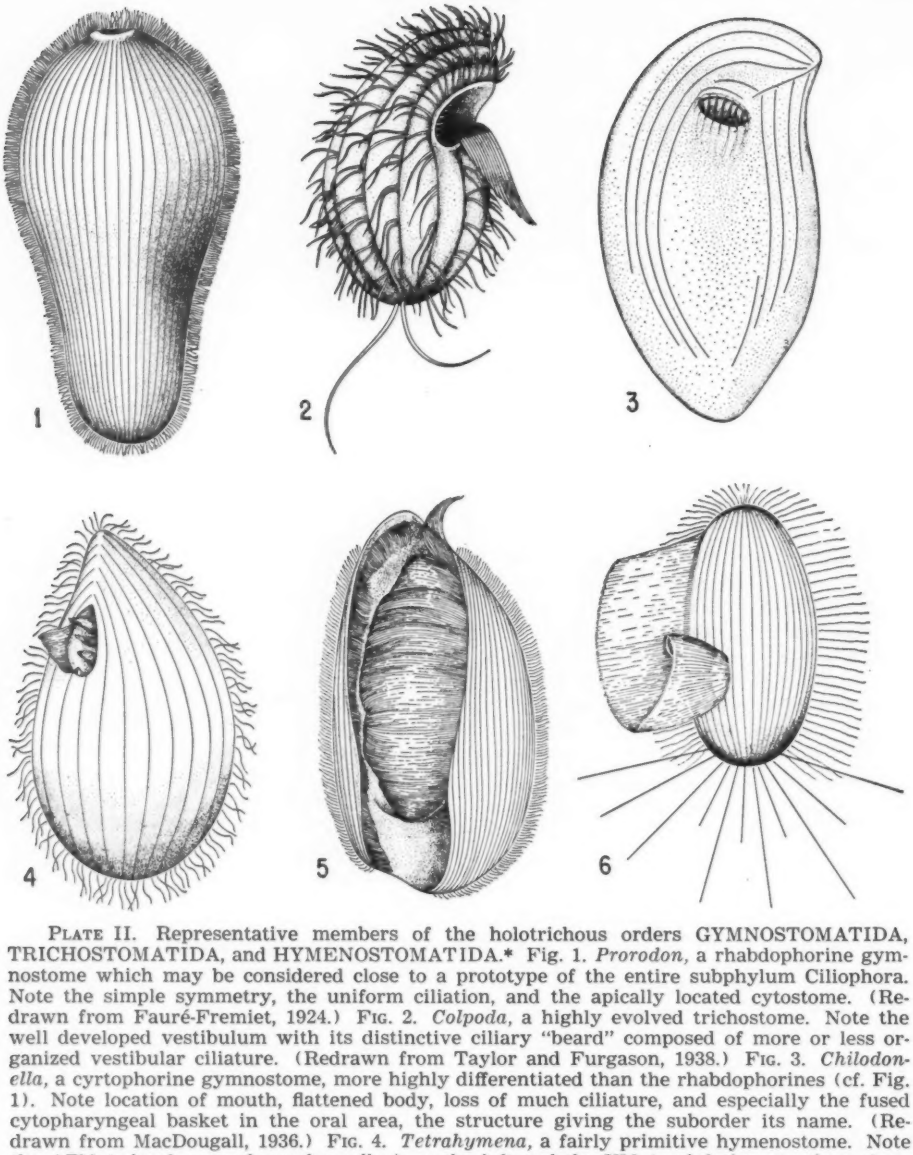

PLATE II. Representative members of the holotrichous orders GYMNOSTOMATIDA, TRICHOSTOMATIDA, and HYMENOSTOMATIDA.* Fig. 1. *Prorodon,* a rhabdophorine gymnostome which may be considered close to a prototype of the entire subphylum Ciliophora. Note the simple symmetry, the uniform ciliation, and the apically located cytostome. (Redrawn from Fauré-Fremiet, 1924.) FIG. 2. *Colpoda,* a highly evolved trichostome. Note the well developed vestibulum with its distinctive ciliary "beard" composed of more or less organized vestibular ciliature. (Redrawn from Taylor and Furgason, 1938.) FIG. 3. *Chilodonella,* a cyrtophorine gymnostome, more highly differentiated than the rhabdophorines (cf. Fig. 1). Note location of mouth, flattened body, loss of much ciliature, and especially the fused cytopharyngeal basket in the oral area, the structure giving the suborder its name. (Redrawn from MacDougall, 1936.) FIG. 4. *Tetrahymena,* a fairly primitive hymenostome. Note the AZM (adoral zone of membranelles) on the left and the UM (undulating membrane) on the right, allegedly representing the first appearance of true buccal ciliature in the Ciliophora; compare with the infraciliary picture in Plate I, Figure 1 (different species but same genus). (Redrawn from Corliss, 1953*b*, modified from Kozloff, 1946.) FIG. 5. *Lembadion,* a more highly differentiated member of the hymenostome suborder Tetrahymenina. Note greatly increased size of the buccal area and the conspicuous membranellar complex on the organism's left. (Redrawn from Fauré-Fremiet, 1924.) FIG. 6. *Pleuronema,* a representative member of the evolved hymenostome suborder Pleuronematina. Note two prime characteristics of the group: hypertelic development of the UM and subequatorial location of the cytostome (not visible here), factors of major phylogenetic significance. (Redrawn from Noland, 1937.)

* The writer wishes to express here his gratitude to Miss Alice Boatright for her painstaking execution of all figures in this paper. The drawings essentially have been copied from the various papers acknowledged as sources; in some cases the original figures have been modified to a greater or lesser extent. External somatic ciliature generally has been shown only peripherally, otherwise rows of cilia have been indicated simply by lines. No attempt has been made to depict the infraciliature, the nuclei, or various cytoplasmic inclusions in the drawings of Plates II, III, IV.

older classification are much more closely related to each other than to the "hypostomes," as Kahl (1930–1935) was actually well aware, and this is indicated in the revised scheme. Indeed, Fauré-Fremiet (1950*a*) has considered the two new subdivisions to be so different that he has considered them as separate orders, namely, the "Gymnostomes rhabdophores" and the "Gymnostomes cyrtophores," unfortunately employing a binary nomenclature and listing the names in a vernacular style only. The writer will list the two groups here as suborders, in a more conservative treatment, with nomenclature based upon the descriptive terminology furnished by Fauré-Fremiet:

Suborder (1) Rhabdophorina Fauré-Fremiet [6]

A large group composed principally of carnivorous gymnostomes. The cytostome, typically appearing directly on the surface of the body and uncomplicated by the presence of a vestibulum or a buccal cavity, structures so characteristic of higher orders, is located either apically or laterally. The morphogenetics of both fission and stomatogenesis is relatively simple, the ciliary meridians or kineties apparently playing equipotential roles in these phenomena.

Of special taxonomic importance are the skeletogenous structures commonly called trichites which line the walls of the cytopharynx of most rhabdophorine gymnostomes. These organelles are arranged in circular fashion but in more or less of a loose bundle, such that they do not interfere with dilation of the cytopharynx when large prey are being ingested.

This suborder contains many species, and no genus can be considered truly typical of the entire group. Common representative genera include *Prorodon* (Pl. II, Fig. 1), *Holophrya, Amphileptus,* and *Dileptus.*

Suborder (2) Cyrtophorina Fauré-Fremiet [6]

A small group of species, all herbivorous and more highly differentiated structurally than the rhabdophorine gymnostomes. The cytostome typically is located on the ventral surface in the anterior half of the body. The kinetosomes of three ciliary rows in the vicinity of the oral opening play a specialized role in stomatogenesis in all cases studied to date (Fauré-Fremiet, 1950*b*).

The cytopharynx is equipped with a more complex type of armature: a fused skeletogenous structure, non-expansible, popularly known as the pharyngeal basket. A reduction in body ciliature is characteristic of the more highly evolved cyrtophorine gymnostomes and some possess a secretory organelle functioning in attachment of the body to the substrate (Fauré-Fremiet and Guilcher, 1947).

Chilodonella (Pl. II, Fig. 3) and *Nassula* may be cited as representative genera.

Order 2. SUCTORIDA Claparède and Lachmann, 1858

A closely knit but enigmatic group, admittedly with few solid clues as to its origin or exact relationship with other existing orders. But on the basis of the new morphological and morphogenetic data, supplied principally by Guilcher (1951), combined with the hypotheses of Chatton and Fauré-Fremiet discussed above, it seems justifiable to consider the suctoria as "good" holotrichs. The general relationship is seen particularly in the pattern of the ciliature (and the infraciliature) in the migratory buds or larval forms.

A number of characteristics of the SUCTORIDA sometimes thought unique

[6] The writer is taking the liberty, with Professor Fauré-Fremiet's permission (granted in a personal communication received in March, 1956), of crediting the nomenclature here used to him, as of the date of this paper. The writer is responsible for the name's use at the subordinal level but certainly credit for first realizing the distinctiveness of the group and for furnishing the descriptive terminology upon which the name finally has been formed is due Professor Fauré-Fremiet.

for several or all suctorian species are shared with other entire holotrichous groups or at least with certain members in those groups: the budding mode of reproduction (also found among chonotrichs, trichostomes, thigmotrichs, possibly certain peritrichs); total transformation of an adult into a larva (see Faure-Fremiet, 1945*b;* also found in peritrichs); the scopula and stalk (also in peritrichs, and homologue, thigmotactic ciliature, in thigmotrichs, hymenostomes, and possibly others, perhaps including the peduncle of the apostome phoront; but note that the stalk of chonotrichs is not homologous); atypical mode of conjugation, shown by some, involving size differences or permanent fusion of conjugants (also in certain thigmotrichs, chonotrichs, peritrichs, and other scattered cases); possession of tentacles (also some gymnostomes, thigmotrichs); a naked non-ciliated stage in the life cycle (also in trichostomes, thigmotrichs, possibly others; and true of the encysted stage in many orders).

The above characteristics of the SUCTORIDA, in spite of their lack of complete uniqueness, when considered as a group do not seem to indicate close affinities with any other single order. Collin (1912) held that they arose from peritrichous forms; Kahl (1931) suggested their origin from prostomatous gymnostomes. Guilcher (1951), upon the basis of her thorough comparative study of many species in which she employed silver impregnation, microcinematography, phase, and even electron microscopy, also concluded that their most likely progenitors were rhabdophorine gymnostome-like ciliates. She did not support Kahl's theory of how this might have come to pass, however, and believed that no homology exists between the tentacles of the two groups. Doflein and Reichenow (1949–1953), in an unprecedented move not followed by other current treatises on the protozoa, dropped the group from class to ordinal rank on the basis of Kahl's hypothesis concerning their phylogeny (see Table I).

It is beyond the scope of the present paper to attempt any further critical discussion of suctorian genealogy. Its holotrichous position in the systematic scheme seems justifiable on the basis of our knowledge to date. One should be cautious in postulating a necessarily close phylogenetic relationship with any other group which happens to possess some similar-appearing structure: some such features may have arisen independently during a very long period of parallel evolution. The scopula and stalk, exhibited by both SUCTORIDA and PERITRICHIDA, might serve as a good example of this danger, for other information appears to show that these two groups, although both on the fringe of the holotrichous sphere, represent very widely separated forms from an evolutionary point of view.

The phylogenetic origin of the suctorian tentacle remains one of the major mysteries of protozoology although modern work with electron microscopy is making it quite clear that the classical idea (Bütschli, 1887–1889) of its representing merely a "drawn out cytostome" cannot be retained. The tentacle appears to be a highly complex, compound organelle, both in its anatomy and its physiology (e.g., see Dragesco and Guilcher, 1950; Guilcher, 1951; Rudzinska and Porter, 1954; Rouiller and others, 1956; Kitching, 1954; Hull, 1954*a*). There was very likely a time in their earliest history when a "proto-suctorian" possessed both a simple cytostome, destined to disappear, and the beginnings of independently developing suctorial tentacles. Possibly the migratory, holotrichous form was the mouthed organism originally and the sedentary, tentacle-developing form arose secondarily at a much later time. This would not be the only example in the Animal Kingdom in which the more recent, attached stage has become the dominant, reproductive one, with preservation of the ancestral motile form as a means of dispersal.

A representative form, probably belonging to the genus *Podophyra* (see Hull, 1954*b*), is depicted in Plate III, Figure 6, showing the relationship of the mature

parental and the budding larval forms; see also Plate I, Figure 3. The genus *Acineta* may also be considered representative of the order.

Order 3. CHONOTRICHIDA Wallengren, 1895

A small group of vase-shaped, sedentary organisms, with apical portion of the body often drawn out into the form of a funnel; traditionally considered nearly as aberrant and exclusive as members of the preceding order. The enigma of kinship with other forms in this case, however, has been resolved with clarity by the same young lady who made such important contributions to our understanding of the SUCTORIDA (Guilcher, 1951). It was particularly her morphogenetic study of ontogeny, employing the nearly indispensable French silver technique, which made it possible for Guilcher to realize that the chonotrichs are closely related to certain cyrtophorine gymnostomes. Older works had been concerned primarily with morphology of the seemingly aberrant attached adult stage.

The migratory form resembles the Cyrtophorina remarkably in the pattern of its ciliature (and infraciliature), confined to the ventral surface and arranged in two fields in both cases; in location of the oral area; in the secretory apparatus responsible for production of the organ of fixation present in all mature chonotrichs and in certain cyrtophorine gymnostomes; and in the highly specialized organization of the macronucleus, nearly identical in members of both groups. By complex morphogenetic movements, painstakingly traced by Guilcher, in which allometric growth of certain areas of the body occurs, the ventral surface of the cyrtophorine-like larval form becomes the anterior end of the attached mature form. In many chonotrichs the metamorphosis is continued until the larval ventral surface becomes pulled out into the remarkable, spiralled, funnel-like shape so characteristic of the order (see Pl. III, Fig. 1).

The "clockwise winding" ciliature of the funnel has been considered as "peristomial ciliature" by protozoologists in general, leading them to place the chonotrichs near the spirotrichs on this basis. Although understanding the origin of the ciliated area, the French workers have retained the term peristome. In the opinion of the writer we have here a valid example of a vestibulum equipped with vestibular ciliature, if one agrees with the definition of a vestibulum as an area of the body, often depressed, in the region of, and leading to, the cytostome (with an intervening buccal cavity in higher orders), furnished with ciliature of purely somatic origin (Corliss, 1955*c*; see also the TRICHOSTOMATIDA, below). Guilcher has demonstrated that the origin of the cilia present in the oral area of chonotrichs is the ciliature of the ventral surface of the body of the "cyrtophorine" stage. Secondary morphogenetic movements bring about its definitive location in the mature form. The simple vestibular ciliature of the chonotrichs, then, is not at all homologous with the highly organized buccal or peristomial ciliary organelles of higher orders (see HYMENOSTOMATIDA, and others, below).

The chonotrichs have also been considered as a group distinct from but near the peritrichs because of the apparently similar mode of attachment, and as near the suctoria because of common exhibition of both the sedentary and the gemmiparous habit. It is now known that the organelle of fixation in the CHONOTRICHIDA is not at all homologous with the scopula and stalk of the PERITRICHIDA and the SUCTORIDA (Fauré-Fremiet, 1905; Fauré-Fremiet and Guilcher, 1947; Guilcher, 1951; Fauré-Fremiet and others, 1956); and asexual reproduction in ciliates by budding, as mentioned in the preceding section, is not confined to the chonotrichs and the suctoria.

Establishment of the evolutionary history and proper taxonomic position of the CHONOTRICHIDA represents an outstanding example of successful application of new morphological and morpho-

genetic data to solution of one of the greatest enigmas in ciliate systematics.

The widely distributed genus *Spirochona*, whose species occur as ectocommensals of fresh-water gammarids, may be considered as representative of the order (see Pl. III, Fig. 1), although all the other genera are marine.

Order 4. TRICHOSTOMATIDA Bütschli, 1889

A heterogeneous collection of some fifteen families, with many of the involved species inadequately described, possessing few distinctive traits in common. The following examples indicate the taxonomic uncertainty surrounding the order: the best known genus, *Paramecium*, is actually a hymenostome and must be removed without question (Fauré-Fremiet, 1949, 1950*a*; von Gelei, 1952; Yusa, 1955; and see the following section); on the other hand, the parasitologically popular "heterotrich," *Balantidium*, should be added to this order (Fauré-Fremiet, 1955), as should also such "representative gymnostomes" as *Coelosomides* and *Pseudoprorodon* (Fauré-Fremiet, 1950*a*,*c*).

Because of the polyphyletic nature of the group as it is currently composed and because of our lack of precise knowledge of the morphology, in particular the infraciliary picture, of many species, it is difficult to characterize the TRICHOSTOMATIDA with any finality. One outstanding feature has been revealed in the forms carefully studied with modern techniques: the universal possession of a well-defined vestibulum, unaccompanied by a true buccal cavity. That is, the vestibulum here, as already noted above for the off-the-main-line chonotrichs, may be considered as a secondarily depressed area of the ventral surface leading directly to the cytostome or true mouth and equipped with somatic ciliature more or less modified but never reaching the high degree of organization typical of buccal or peristomial ciliature (cf. Figs. 2 and 4 in Pl. II, and see HYMENOSTOMATIDA, below).

Stomatogenesis, as well as fission, has become a more elaborate process in the trichostomes, as compared with the condition found in the majority of the rhabdophorine gymnostomes, which are probably the present-day representatives of the trichostomes' immediate ancestors. The complications have arisen because of the presence of the vestibulum and, typically, a more highly asymmetrical body form. The morphogenetics of these phenomena, an understanding of which is so important from the phylogenetic-systematic point of view, has been beautifully investigated in advanced trichostomes by Taylor and Garnjobst (1939) (who, however, considered the vestibular ciliature to be organized into true buccal membranelles), and by Tuffrau (1952). Differentiation in the order seems to have reached a peak in the complex species of *Colpoda* and *Tillina*, the genera studied by the workers just mentioned, yet in their ontogeny the conditions typical of the simplest gymnostomes are clearly recapitulated. The highly asymmetrical mature forms, equipped with well-developed vestibulum and vestibular ciliature, encyst, undergo complete dedifferentiation of all ciliature, assume a form with radial symmetry, and undergo one or two fissions of a straightforward perkinetal type. Stomatogenesis, allometric growth of certain (dorsal) kineties, torsion imposed by involved morphogenetic movements, excystment—these phenomena allow realization once again of free-swimming, mature forms (see Pl. I, Fig. 2).

Genera representative of the lower trichostomes should include *Coelosomides;* of the higher forms, *Tillina* and *Colpoda* (see Pl. II, Fig. 2). The recent excellent description (Tuffrau, 1954) of a member of the curious family Trichopelmidae, in which an affinity with the cyrtophorine gymnostomes was postulated for the organism, serves to emphasize the polyphyletic origin, already noted at the beginning of this section, of the TRICHOSTOMATIDA as currently composed.

Order 5. HYMENOSTOMATIDA Delage and Hérouard, 1896

A group of "membrane-mouthed" holotrichs which appear to occupy a central position in the phylogeny of ciliates, standing also about midway in the list of ciliophoran orders with respect to numbers of species. The evolutionary lability or mutability of the order seems to be reflected in the diversity shown by its species, particularly in regard to mouth structures and modes of stomatogenesis. On the one hand, the hymenostomes are relatively undifferentiated ciliates, typically small in size and uniformly clad in cilia; on the other, they may be considered to be the first holotrichs to have evolved a buccal cavity, an area defined by its possession of true buccal (or peristomial) ciliature: the adoral zone of membranelles (AZM) and the undulating or paroral membrane (UM), or their alleged homologues. Since the hymenostomes appear to stand at a major crossroads, as it were, in ciliate evolution, it is fitting to consider them in a little more detail.

Extensive investigation of the characteristics in the area of the mouth and of the role of the phenomenon of stomatogenesis, carried out to date on a large scale chiefly by French [7] protozoologists, makes possible the recognition of three types of buccal apparatus among the hymenostomes, as Fauré-Fremiet (1950*a*) has pointed out. Although much more work on scattered species remains to be done, it is the writer's belief that these three categories already may be considered of sound subordinal value; further discussion of the evolutionary and phylogenetic significance of the HYMENOSTOMATIDA, then, will be presented under these three headings.

Suborder (1) Tetrahymenina Fauré-Fremiet [8]

A large group, including generally small, relatively undifferentiated species, with the compound ciliary organelles of the buccal area arranged in a primitive, tetrahymenal pattern: three membranelles, primarily on the left, composing the typically inconspicuous AZM, and a single undulating membrane (UM), likewise generally inconspicuous, on the right (see Pl. I, Fig. 1; Pl. II, Fig. 4). It should be pointed out that not all species conform perfectly to this description: in the macrostome form of *Tetrahymena patula*, for example, the UM is prominently developed (Furgason, 1940; Fauré-Fremiet, 1948*b*; Corliss, 1953*c*). In genera like *Glaucoma* the three bases of the AZM are no longer all on the left (Furgason, 1940; Corliss, 1954; von Gelei, 1936). And in a number of genera the AZM secondarily may be thrown entirely over to the right, up against the UM (Mugard, 1949). Finally, in some species the ciliature of the alleged AZM-complex is far from being inconspicuous (for an outstanding example see Pl. II, Fig. 5).

The true mouth, the cytostome, lies at the bottom of the buccal cavity, leading directly into the cytopharynx. The buccal

[7] Among the prolific works of the great Hungarian protozoologist József Gelei are a number of significant contributions to our knowledge of the biology of hymenostome ciliates, including information about their buccal and somatic infraciliature. All of these cannot be cited directly in the present paper but the interested reader is referred to the complete list of J. von Gelei's papers published by Gellért and Müller (1954) in the *Gedenkschrift* issue of the *Acta Biologica*. A particularly stimulating and well-documented discussion on the structural and functional diversification among ciliates at the organellar level, with regard to the morphogenetical principles of Sewertzoff, may be found in von Gelei (1950).

[8] As above (see footnote 6), the writer is taking the liberty, with Professor Fauré-Fremiet's permission (granted in a personal communication received in March, 1956), of crediting the nomenclature here used to him, as of the date of this paper. The writer is responsible for the name's use at the subordinal level but certainly credit for first realizing the distinctiveness of the group and for furnishing the descriptive terminology upon which the name has finally been formed is due Professor Fauré-Fremiet.

cavity, which contains the bases of the four membranous organelles comprising the tetrahymenal buccal apparatus, typically opens, through the buccal overture, directly onto the surface of the body. In some of the more highly evolved forms, such as species of the genus *Ophryoglena,* the buccal cavity is so depressed that a true vestibulum, adorned solely with somatic ciliature, may be said to be present as well. Incidentally, the well-known genus *Ichthyophthirius,* often considered a gymnostome, possesses mouth parts in the mature form which place it in the present suborder without question.

It is of interest to note that an astomatous ciliate has recently been allocated to a family of this suborder (Kozloff, 1954). This rather iconoclastic taxonomic move appears justifiable: the general pattern of the somatic infraciliature of the organism, for example, in spite of its mouthless condition, is identical with that of species of such hymenostome genera as *Tetrahymena* (for further consideration of this case see ASTOMATIDA, below).

The mode of stomatogenesis varies from group to group within the Tetrahymenina. *Tetrahymena,* here designated the type species, possesses a single stomatogenous meridian or kinety, the so-called kinety number 1 (see Pl. I, Fig. 1). Two such kineties are involved in *Deltopylum,* many in *Ophryoglena.* In forms like *Philaster, Anophrys,* and *Paralembus* a little understood type of "director-meridian" appears to play a role in the morphogenetics of new mouth formation (von Gelei, 1934*c*; Mugard, 1949). Cases involving a single stomatogenous meridian have been most studied (Chatton *et al.,* 1931; von Gelei, 1935; von Gelei and Horváth, 1931; Klein, 1927, 1928; Furgason, 1940; Mugard, 1949; Corliss, 1953*c*).

The main evolutionary line of the Ciliophora may well have passed through this group sending off branches to the right and left as it continued "upward" to the spirotrichous ciliates (see Table II, a proposed phylogenetic tree, and attendant discussion. Such speculation, based upon the Furgason-Fauré-Fremiet hypothesis (see p. 75), is not entirely unfounded, as comparative study of many cases among the hymenostomes and the heterotrichs, the principal groups involved, will show (Villeneuve-Brachon, 1940; Mugard, 1949). Whether the phylogenetic origin of the greatly increased number of component parts of the AZM in the subclass Spirotricha can be traced to the mode of duplication seen in the ontogeny of *Porpostoma,* where the base of membranelle number 1 undergoes elongation and segmentation into many more or less clearly separated parts or pseudomembranelles, remains a debatable but very interesting possibility.

In addition to the indications that the Tetrahymenina served as the evolutionary springboard for the more highly evolved spirotrichous ciliates, there is a strong possibility that the other hymenostome suborders, the Peniculina and the Pleuronematina, arose quite directly from this group. Thus the primitive tetrahymenal hymenostomes also would represent the parental stock, through the Pleuronematina, of the orders THIGMOTRICHIDA and PERITRICHIDA. It is furthermore possible that the aberrant groups represented by the ASTOMATIDA and the APOSTOMATIDA had their ancestry among members of this suborder of hymenostome holotrichs; if such can ever be proven to have been the case, then the Tetrahymenina may indeed be looked upon as a major pivotal group in the evolution of the Ciliophora.

Suborder (2) Peniculina Fauré-Fremiet [8]

A highly evolved group of hymenostomes, showing a degree of complexity in their buccal organelles considerably advanced over the primitive tetrahymenal organization characteristic of the preceding suborder. The key structure here is the peniculus, a compound ciliary organelle postulated to be homologous with a single membranelle in the AZM of the basic tetrahymenal type. The peniculi,

always more than one in number, occur in a position in the buccal cavity (generally called the pharynx in the literature on *Paramecium*) which supports the alleged homology. Species included here may possess a well-defined vestibulum in addition to the ever-present buccal cavity.

The mode of stomatogenesis characteristic of the entire suborder appears to be of an autonomous type. That is, the mouth structures of the posterior daughter, the *opisthe*, appear to depend for their origin upon part of the infraciliature of the parental buccal apparatus (which is passed on intact to the anterior daughter, the *proter*). This represents quite an advance over the situation known for the most primitive hymenostomes, like *Tetrahymena*, where buccal *anlagen* are dependent upon the somatic infraciliature of specific stomatogenous kineties.

The *Paramecium* story, yet to be told in full (Yusa, 1955), is worthy of brief mention here since this commonly known genus, still considered a trichostome in current textbooks, may well be designated as the type of the Peniculina. *Paramecium* has two peniculi, an enigmatic quadrulus (*membrana quadripartita* or *vierermembran* of the literature) and an often overlooked endoral membrane. In the writer's opinion (see also Yusa, 1955) the quadrulus, suggested as homologous with the UM of simpler hymenostomes by Fauré-Fremiet, is more likely either a highly modified membranelle or a buccal structure unique in this suborder. Von Gelei's (1934*a*,*b*) endoral membrane, on the other hand, appears definitely to be the UM homologue in *Paramecium*. According to the precise work of Yusa (1955), not yet published in full, the *anlagen* of all the buccal organelles of the opisthe are in some manner associated with the parental endoral membrane in their origin. The location of this organelle on the right side of the buccal cavity just inside the buccal overture (at the base of the vestibulum) also suports the homology. Further, the allegation fits the postulated evolution of the autonomization of mouth parts in stomatogenesis, commencing with true stomatogenous kineties and passing through the "director-meridian" type known for *Philaster*, *Anophrys*, and others, since in all the types of stomatogenesis known among the higher holotrichs there appears to be a more or less close *rapport* with the UM.

The removal of *Paramecium* from the TRICHOSTOMATIDA has been a taxonomic matter actually under consideration for some years. In his classical paper on the detailed structure of mouth parts in this genus, von Gelei (1934*b*) realized that *Paramecium* was not a typical trichostome, but he thought its possession of a vestibulum excluded it from the hymenostomes. He suggested erection of a new taxon to contain it, the TRICHOHYMENOSTOMATA, but offered little detail concerning systematic aspects of the matter. In a later paper, published posthumously, von Gelei (1952) came to the conclusion, independently of Fauré-Fremiet's published views on the subject, that *Paramecium* should be considered a true hymenostome, "near *Frontonia*," in a group to be called the "Vestibulata." (The writer's views concerning the significance of the vestibulum in ciliate phylogeny differ from those of von Gelei, but discussion of the matter is beyond the scope of the present paper.)

Highly differentiated hymenostome genera other than *Paramecium* which have been studied adequately enough with silver impregnation techniques to provide some information concerning the infraciliary picture of their buccal apparatus in its definitive and developmental stages include *Frontonia*, *Stokesia*, *Disematosoma*, *Urocentrum*, and *Espejoia* (Fauré-Fremiet, 1949, 1950*a*, 1954*a*; Fauré-Fremiet and Mugard, 1949*a*; von Gelei, 1950, 1954). In the writer's opinion, *Espejoia* and possibly *Urocentrum*, the French studies of which may need a little reinterpretation, may serve as linking genera between the more primitive of the Tetrahymenina and the most

highly evolved members of the Peniculina. Perhaps the species most in need of precise study from the point of view of buccal infraciliature are those of the large and widely distributed genus *Frontonia*.

Suborder (3) Pleuronematina Fauré-Fremiet [8]

A small group of genera showing evolutionary advance over the Tetrahymenina yet lacking the "dead-end over-specialization" seen in the Peniculina. Distinctive characteristics involve the hypertelic development of the right-hand UM, the typically subequatorial position of the cytostome, and the presence of an area, dorsolateral in location, of thigmotactic ciliature. The AZM-complex is not as clearly defined as it is in the majority of the species in the suborder Tetrahymenina. Considerably more work needs to be done on the Pleuronematina, even regarding the exact boundaries of the group, with the refined techniques now available, although a solid foundation has been laid in the precise investigations of Hoare (1927), a paper often overlooked, and of Kahl (1926, 1930-1935), Noland (1937), and Párducz (1936, 1940).

The characteristics briefly described above represent significant factors in the phylogenetic history of the suborder itself; they are even more important in relation to orders neighboring the HYMENOSTOMATIDA. Such genera as *Pleuronema* (see Pl. II, Fig. 6) and *Cyclidium*, representative of the group, may well have figured in the evolutionary origin of the THIGMOTRICHIDA and the PERITRICHIDA, orders to be discussed presently.

Order 6. ASTOMATIDA Schewiakoff, 1896

An aggregation of mouthless ciliates long recognized as comprising a heterogeneous group, their very diversity indicative of a polyphyletic, although unknown, origin. The problem of their true evolutionary relationships has been brought into sharp focus by the appearance of two very recent publications. Kozloff (1954), in a short but excellent work, has transferred an astomatous form to the family Tetrahymenidae (HYMENOSTOMATIDA) on the basis of its infraciliary structures, in spite of its lack of mouth and buccal organelles. This act seems justifiable and commendable. De Puytorac (1954), in a monographic cytological and taxonomic study in which silver impregnation was extensively employed, examined some seventy-five species and reached several conclusions of great pertinence to the present discussion. The French worker, who for the most part examined only astomatous ciliates symbiotic in annelids, the metazoa, which, however, serve as hosts for the majority of forms conventionally assigned to the order, has suggested that the group name should be suppressed altogether, since, in his opinion, most of the known species are either thigmotrichs or degenerate apostomes. These conclusions are based upon his analysis of data concerning life histories and host relationships, his study of the nature of the infraciliature, and his comparison of other minor morphological or developmental features of both the "astomes" he investigated and representative species of the two orders to which he would allocate the majority of astomatous holotrichs.

It is the belief of de Puytorac that the few species of astomes which have been described from Turbellaria and Amphibia form "a homogeneous group of unknown origin," but he does not suggest what ordinal name might be employed for them. Unfortunately he did not study these forms personally, nor did he have an opportunity to examine species from molluscs such as the form from the freshwater limpet which was redescribed in Kozloff's interesting paper cited above.

Whatever their origin, the nearly two hundred species of so-called astomes show a considerable diversity of form

and, in some groups, an elaboration of intricate holdfast organelles and endoskeletons of scleroprotein (Cheissin, 1930; Rossolimo and Perzewa, 1929; de Puytorac, 1951). Their common lack of a mouth, it must be emphasized, is of secondary importance, having doubtless come about in parallel with their adaptation to an endosymbiotic existence, and is a negative characteristic from the point of view of systematics. This is stressed because of the weight some protozoologists, even in modern times, have placed upon a mouthless condition: for example, Calkins (1933), who adamantly retained even the opalinids in the ASTOMATIDA solely on the basis, and certain current textbooks, which imply that the astomes are the most primitive of ciliates for the same weak reason.

The writer is in general sympathetic with the taxonomic conclusions of de Puytorac, an acknowledged modern authority on these ciliates. Is it not perhaps reasonable to suppose, however, in regard to the majority of forms considered by de Puytorac to have arisen from thigmotrichs, that a long evolutionary history since their separation might justify the preservation of a separate ordinal name for these species? And if one agrees that thigmotrichs have arisen from hymenostomes (see below) could not most of the present day astomes possibly have originated independently from the same ancestral order, the HYMENOSTOMATIDA, coming to resemble certain THIGMOTRICHIDA during a long period of parallel evolution?

The few forms considered degenerate apostomes could well be transferred to that order. And certain species clearly hymenostome in nature, as in the case described by Kozloff, can be reallocated to the HYMENOSTOMATIDA, notwithstanding their mouthless condition.

This leaves the knotty problem of the *Haptophrya* group, well known in the United States through several fine cytological researches on American species. Has their origin been from the primitive GYMNOSTOMATIDA, with subsequent specialization in the adaptation to a symbiotic life; or from the tetrahymental HYMENOSTOMATIDA or some other even more highly evolved group, with degeneration of certain complex structures and appearance of novel ones? Should the name and the order "ASTOMATIDA" be reserved exclusively for just these forms, perhaps?

Much more research is needed to answer all the questions still posed by this heterogeneous assemblage of mouthless holotrichs.

Among well known representative genera of de Puytorac's thigmotrich-derived group may be listed *Anoplophrya, Radiophrya,* and *Hoplitophrya;* from the small group having amphibian or turbellarian hosts, the genus *Haptophrya* may be mentioned.

(To be concluded)

Points of View

Clarification of Certain Aspects of Infraspecific Systematics

Certain criticisms have been published by Brown and Wilson (1954) concerning the views expressed in my article (1954) entitled "A new approach to infraspecific categories." Most of their statements demand refutation, lest they result in unnecessary loss of confidence in my proposals.

These critics chide me for seeming to "lean toward the vogue, especially popular in Russia earlier in this century, dictating that there are several fundamentally different kinds of infraspecific populations." I can hardly imagine a modern systematist failing to realize that such different categories do exist, yet the accusation that I am "prey to similar basic confusion" implies that here are two authors who do! The personal expressions by Wilson and Brown concerning that to which they refer as my "philosophical exercise," and their strong stand against any position short of complete abolition of the subspecies category are probably best accepted as manifestations of their extreme enthusiasm for their own proposal. (Their proposal may be summed up in the simple statement: "eliminate trinominals completely.")

We are confronting a grave crisis, and the future of systematic zoology will be tremendously affected by the judgement of our contemporaries. I hope that the most rational and durable opinions will prevail and that a tenable position can be agreed upon before we are hopelessly engulfed by the growing confusion in infraspecific systematics. It is because of my sincere concern and alarm that I feel obliged to defend the portions of my article which were assailed by Wilson and Brown and to attempt to reconcile the differences of opinion which elicited their faintly caustic attack.

These critics disagree with my contention that the subspecies is a definable category. In essence, I defined subspecies as "natural, obviously different populations, the members of which would crossbreed rather freely *if* they occurred sympatrically and synchronically under natural conditions, but which are distinctly separated spatially, ecologically, or temporally during their mating periods." Wilson and Brown state that "in making this proposal, Edwards ignores the central argument against the objective subspecies: (1) the apparent universality of non-concordance in geographic variations, and (2) the extreme arbitrariness inherent in the delimitation of populations in terms of real or presumed geographic discontinuities." I found it necessary to engage in lengthy correspondence with Dr. Brown in order to learn the reasons for some of his statements, and he has cooperated so well that I am now able to explain his inability to understand portions of my article and his reluctance to agree with other portions of it.

By "concordance," Wilson and Brown mean "the degree to which the variation of genetically independent characters is correlated over the entire distribution of the species" (Brown, personal correspondence, 1955). This definition is so important a part of their criticism of the subspecies category that it deserves special consideration here. It implies that if there is even the slightest degree of failure of every character to display absolute correlation with every other character possessed by the members of local populations comprising any species, then

there is "non-concordance." This is probably true of every infraspecific category in existence, because differences in genetically fixed characters are constantly developing in every population. Mutations occur in every generation and are usually either favorable or unfavorable, depending upon selective or environmental factors.[1] If the range of the population is so uniform that no adaptive differences result from environmental impact upon the local demes, there still may be genetic differentiation throughout the species range because of non-adaptive gene changes[1] or (in very small populations) because of gene drift.[2] If any gene occurs in two or more allopatric or allochronic populations of a species, the reason must be one of the following: (1) that gene is one responsible for the distinctive characteristics of the species, genus, and higher taxa of the populations involved; (2) the gene is neutral in its selective and survival value; (3) the respective populations have not been isolated long enough for the gene to be eliminated from the gene pool of either; or (4) the isolated populations have each acquired the same gene, through independent mutations. This is true not only of one gene but for all genes in the gene pool, therefore any populations which would fit my proposed subspecies definition are practically certain to display non-concordance. By definition, these "subspecies" are prevented from interbreeding, hence any mutation that occurs will be prevented from spreading to other "subspecies" of this type. Despite my critics' concern over the "apparent universality of non-concordance in geographic variations" there is really no reason to ever expect complete concordance of all characteristics of local populations within any species! Genetically independent characters will not all vary gradually from one extreme to another at opposite ends of a *rassenkreis,* even when there are not definite steps along the cline. When there is some correlation it need not be linear but may instead be correlated directly with environmental differences and their influence upon certain genetically fixed characters. Between any two demes there will be good correlation of some characters and lack of correlation of others, depending upon which of the influencing factors enumerated above are operative in that particular situation. If there is not complete concordance, obviously there must be some degree of non-concordance, so the "universality of non-concordance" is really a constant characteristic feature of all allopatric and allochronic populations of animals.

To summarize, I agree that Wilson and Brown are correct in pointing out the universal lack of concordance of genetic variation between recognizable infraspecific populations, but I fail to understand their reasons for considering this fact an "argument against the objective subspecies."

To dispose of the second of my critics' "central arguments" I feel that I need only point out that it is easier for a systematist to be positive about geographic or temporal discontinuities between populations than it is for him to be equally positive about reproductive discontinuities between populations which are commonly regarded as distinct species. Hubbs (1955) calls attention to dozens of instances in which there is partial breakdown of the reproductive isolating mechanisms which normally keep species of fish from interbreeding. Numerous other examples of hybridization between members of different species or genera or even families or phyla have been discussed in biological literature. Despite this well-documented knowledge, there are few systematists who would favor discarding the species category just because of the

[1] E. B. Ford (1945) maintains that no genetic change in evolution can be wholly non-adaptive, even though that impression may be created because of the pleiotropic effects of very many genes.

[2] R. A. Fisher and E. B. Ford (1947) believe that no demes small enough to allow the action of Sewall Wright's "drift" are sufficiently permanent to have any evolutionary value.

difficulty and arbitrariness inherent in the delimitation of populations in terms of real or presumed reproductive discontinuities. Why then should this difficulty in delimiting subspecies (as I propose to define them) be considered so drastic, when the species upon which systematic studies are primarily based are at least equally difficult to delimit? Unless Wilson and Brown also recommend eliminating the species as a taxon, how can they honestly condemn my "subspecies" which is less arbitrary and less difficult to delimit than the present species category? We must admit that all borderlines in systematic zoology are vague, then strive to establish definitions that are as objective as possible under the circumstances. I believe that my proposed definition of subspecies fulfills that requirement as well as any which could possibly be devised.

Now that I have shown that neither of my critics' arguments against the objective subspecies can be directed with honesty against my proposed definition, I hope that taxonomists engaged in the controversy concerning infraspecific categories will continue to give my proposals their sincere consideration. I cannot agree with Wilson and Brown that there should be no subspecies with taxonomic priority any more than I can accept the prevalent current belief that all slightly different populations (even the almost indistinguishable portions of clines) should be allotted trinominals with international and irrevocable recognition.

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A Note on the Relationship of the Hemipteroid insects

Published phylogenetic classifications of insects are many and varied; some exhibit complete disagreement on the placement of whole blocks of orders, whereas others differ in minor details especially on the little known groups. On the one hand, as Williams (1951), demonstrates, several natural schemes of classifications of organisms are possible and can be considered correct; that is, several could be correct if the differences are only a matter of opinion between the lumper and the splitter. On the other hand the placement of entire phyletic lines of orders is a basic thing and involves as much circumstantial corroboration as it is possible to gather.

Bradley (1946), Ross (1955), and others, consider the orders Corrodentia, perhaps the Zoraptera, the Phthiraptera (Mallophaga-Anoplura), the Thysanoptera, and the Homoptera-Hemiptera as members of a single, compact phyletic line, and not as a subdivision of the orthopteroids. Rather, they suggest that these hemipteroids are a full division and may stand as near to the neuropteroid orders (Holometabola) as to any other major group of orders. Both the aforementioned authors have seemingly well

proved their separation of the hemipteroids and Bradley has presented a long list of features to show that his contentions are based on much circumstantial evidence.

To this list I should like to add another item of proof that the hemipteroids are a real unit that has affinities with the neuropteroids. That item is the characteristic absence of true ocelli in the immature stages of every member of the hemipteroid line. Furthermore, this characteristic is shared with the neuropteroids (Ross 1955), but not with the orthopteroids.

For several years I have examined many collections of psocids, thrips, and bugs, and have never observed the presence of true, functional ocelli in any immature instar. Young of the Phthiraptera never have ocelli, and neither, of course, do the adults. In the orthopteroids, by contrast, whenever adults possess ocelli the immature stages almost invariably have them also.

The lack of ocelli in the larvae of neuropteroids is a well-known characteristic. Apparently the absence of ocelli is also a feature of the pupae (Ross 1955). This characteristic absence of ocelli in any of the immature forms applies equally to the hemipteroids and should be included in the definition of the hemipteroid line.

Thus, the hemipteroids would seem to belong nearest the neuropteroids, to judge from the absence of ocelli in the immature forms as well as from the many other similarities between these two major groups.

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Editor,
SYSTEMATIC ZOOLOGY:

This is a brief semasiological comment on Mr. Follett's excellent résumé of the "Copenhagen Decisions on Zoological Nomenclature" (*Syst. Zool.*, *3*:172).

His mention, in the third paragraph of his article, of "a principle of conservation (sometimes called 'prescription')" might cause the erroneous impression that these two terms are, at least in the connection here concerned, synonymous.

However, in the discussions preceding the Copenhagen Decisions "prescription" has been used with its legal meaning, that is, in Roman Law, "the operation of the law whereby rights might be acquired or extinguished by limitation of . . . time . . .", or, in Civil Law, "the operation of the law whereby rights might be established by long exercise of their corresponding powers (acquisitive prescription) or extinguished by prolonged failure to exercise such powers (extinctive prescription)" (Webster, 2d ed., 1947, p. 1954).

Thus, the conceptual relation between the two above terms, far from being synonymy, is that conservation of "a name in common use" is brought about by acquisitive prescription in its favor and, simultaneously, by extinctive prescription put into operation against the "long-unnoticed senior synonym" to which otherwise the former name would have to yield.

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People and Projects

We note with regret the death of Professor Alfred C. Kinsey of the University of Indiana. Professor Kinsey is well known to his fellow members of the Society of Systematic Zoology for his now classic studies of the systematics of gall wasps. The results of his recent studies of human behavior have reached a far wider audience.

Several noteworthy publications on the collection and preservation of biological material have recently been received.

Biological Materials, Part I, Preserved Materials and Museum Collections, by E. Mayr and R. Goodwin. Publication 399, National Academy of Sciences—National Research Council; 20 pp.

Manual of Tropical Herpetological Collecting (second ed.), by G. S. Myers. Circular No. 4 (mimeographed), Natural History Museum of Stanford University, Stanford, Calif. 13 pp.

Brief Directions for Preserving and Shipping Specimens of Fishes, Amphibians and Reptiles (second ed.), by G. S. Myers. Circular No. 5 (mimeographed), Natural History Museum of Stanford University, Stanford, Calif. 3 p.

The Entomology Department, Bishop Museum, Honolulu, is embarking upon a systematic entomological survey of the southwestern Pacific islands that are considered to be the principal source areas of the Oceanic or Micropolynesian insect fauna. The areas where collecting will be done include the Solomons, Bismarcks, New Guinea, eastern Indonesia, and the southern Philippines. Emphasis at the start will be on New Guinea, the Bismarcks, and Bougainville. The program is being aided by a grant of $23,000 from the National Science Foundation, and is under the charge of J. L. Gressitt.

Three publications in the field of entomology have recently been received from the University of California Press, in the "University of California Publications in Entomology" series.

A Revision of the Psychodidae (Diptera) in America North of Mexico, by L. W. Quate. No. 3 of Volume 10, pp. 103–273, 105 text figs. Price $2.50.

A Systematic Study of the Genus Aphytis Howard (Hymenoptera, Aphelinidae) with Descriptions of New Species, by H. Compere. No. 4 of Volume 10, pp. 271–320, 19 text figs. Price $0.75.

Morphology and Biology of Sturmia Harrisinae Coquillett (Diptera), a Parasite of the Western Grape Leaf Skeletonizer, by O. J. Smith, P. H. Dunn, and J. H. Rosenberger. No. 5 of Volume 10, pp. 321–358, 25 text figs. Price $0.50.

Quate's study of the "fuzzy little gnats" which are the psychodids comprises keys to, and descriptions of, the adults of North American species, and such descriptions of immature stages as are available. All hymenopterans of the genus *Aphytis* parasitize armored scale insects; indeed, as they are the most common parasites of these scale insects, they are important in the biological control of these economically serious pests. Compere's paper presents a useful classification of the North American species based on the coarse characters of the adult as they are evident in museum specimens. As *Sturmia harrisinae* is the most important parasite introduced into southern California to combat its prey, the third paper of this series will be of interest to those interested in the biological control of pest populations.

SYSTEMATIC ZOOLOGY is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Consult recent issues for the style to be followed in the preparation of manuscripts. Contributors are encouraged to submit line drawings and diagrams to illustrate their articles. Half-tones may be accepted where necessary to the article.

Contributors receive galley proof but it is called to their attention that changes made in proof are expensive. The cost of alterations made in proof will be charged to the author if they exceed ten percent of the cost of composition.